ANNALS OF CARNEGIE MUSEUM
VOL. 71, NUMBER 3, PP. 143–213 16 AUGUST 2002

REVISION OF THE NEW WORLD ABARIFORM GENERA *NEOTALUS* N.GEN. AND *ABARIS* DEJEAN (COLEOPTERA: CARABIDAE: PTEROSTICHINI (AUCTORUM))

KIPLING W. WILL[1]
Research Associate, Section of Invertebrate Zoology

ABSTRACT

New World ground beetles (Coleoptera: Carabidae) in the abariform genus-group are classified into three genera, *Pseudabarys* Chaudoir, *Neotalus* new genus and *Abaris* Dejean. Species of the clade *Neotalus* + *Abaris* are revised. Based on the cladistic analysis of adult characteristics, a preferred hypothesis groups species of *Abaris* into clades that are designated as two subgenera and four species-groups: *Abaris sensu stricto* containing three clades designated as species-groups; *A. striolata, A. aenea,* and *A. picipes*-groups and subgenus *Abaridius* Chaudoir (type species *Abaris tachypoides*) comprised of the *A. tachypoides*-group and two species placed *sedis mutabilis* within the subgenus. Seventeen new species are described in the genus *Abaris: A. napoensis, A. bicolor, A. nitida, A. nigra,* from Ecuador; *A. franiai, A. inflata, A. convexa, A. inaequaloides, A. wardi,* from Bolivia; *A. impunctata, A. nobilis,* from Brazil; *A. metallica* from Venezuela; *A. retiaria,* from Colombia and Venezuela; *A. erwini* from Peru and Bolivia; *A. opaca,* from Peru, Bolivia and Brazil; *A. mina,* from Argentina, Brazil, Bolivia, and Paraguay; and *A. aquilonaria* from Central America and Mexico. *Abaris darlingtoni* Straneo and *A. aenea* Dejean are synonymized, the latter is the senior, and hence valid name of the species. The genus *Neotalus* is described to include *N. portai* (Straneo); the species was originally included in *Bothynoproctus* Tschitschérine. Descriptions, distributional information, illustrations of morphological structures, and a key to *Neotalus* and *Abaris* species are provided. Distributional patterns show differences between the *A. picipes*-group species and their sister clade the *A. aenea*-group, with the former being more eurytopic and generally adapted to drier habitats. Biogeographical analysis of biotic zones, using items of error as the optimality criterion, relative to the phylogenetic hypothesis for *Neotalus* + *Abaris*, suggests South American diversification and restriction until at least the Pliocene. *Abaris* species have probably moved into Central America and Mexico four to five times since the development of the land connection with South America in the Pliocene. This contrasts against the biogeographical pattern for *Coptodera* Dejean species (Lebiini), which appear to have basally diverged among the northern areas of Mexico versus South America.

KEY WORDS: New species, systematics, biogeography, classification

INTRODUCTION

Members of the Neotropical genera *Neotalus* new genus and *Abaris* Dejean are small ground beetles (Coleoptera: Carabidae), most individuals are brilliantly metallic with very prominent eyes (Fig. 1). *Abaris* species are uniquely characterized among all Pterostichine grade taxa by pectinate claws (Fig. 2A). These characteristics give them a unique look that is approached in *Pseudabarys* Chaudoir, 1873 and *Prosopogmus* Chaudoir, 1865, both presumed to be closely related genera. I discovered from examination of museum specimens that many more species than the nine named forms of *Abaris* existed. The captivating form and unstudied diversity were the starting points for an interest in revising this group.

A small body of literature treats the abariform species. Straneo (1939) published a key to the eight then named species of *Abaris* and Bousquet (1984) added a

[1] Department of ESPM, Division of Insect Biology, University of California, Berkeley, CA 94720-3112, e-mail: kiplingw@nature.berkeley.edu.
Submitted 10 October 2001.

Fig. 1.—Photograph of living *Abaris splendidula* (LeConte). Collected in Cochise Country, Arizona.

ninth species when he discovered that LeConte's *Pterostichus splendidulus* belonged in the genus *Abaris*. Bousquet and Liebherr (1994) summarized what little had been published on the relationships of the genus *Abaris* and covered nearly all the genera included herein. The complex of genera thought to be closely related and/or associated in published classifications (Bates, 1882; Blackwelder, 1944; Straneo, 1977, 1979; Csiki, 1930; Reichardt, 1977) includes the Nearctic-Neotropical genera *Abaris, Abaridius* Chaudoir, *Ophryogaster* Chaudoir, 1878, *Pseudabarys*; the northern African-Palearctic genus *Orthomus* Chaudoir, 1838; and the Australian genus *Prosopogmus*. My previous analysis of both adult and larval characters (Will, 2000) supports a close relationship of these genera, as well as *Blennidus* Motschulsky, 1866, *Oribazus* Chaudoir, 1874, *Dyschromus* Chaudoir, 1835, *Abacillius* Straneo, 1949 (referred to in Will, 2000 as "genus E"), and *Argutoridius* Chaudoir, 1876. These genera form, in part, a clade centering on the subtribe Euchroina (auctorum) and the *setalis* series (Moore, 1965).

An exceedingly short or absent coronal suture in the larva was considered by Bousquet and Liebherr (1994) as a potential synapomorphy for *Abaris* and *Orthomus* species. This condition is also found in *Pseudabarys* (Will, 2000) and is a significant character for a clade including some or all of the taxa above.

The combination of large eyes, pectinate claws, and metallic luster suggests that *Abaris* species may have peculiar life histories or behaviors relative to related genera that have characteristics more typical for pterostichine grade taxa. However, the limited field observations for these species do not provide incontrovertible evidence for any adaptive significance for this suite of characteristics. In fact, observations of any sort exist for very few of these beetles. Specimens of these species are uncommon in collections. In addition to my own field work, some recent efforts by carabid collectors such as T. L. Erwin (USNM) and G. E. Ball (UASM) have resulted the in collection of large numbers of specimens from a few locations in Central and South America. I hope this monograph will provide researchers and students, particularly those in South America, with the tools to

identify and study species of *Abaris* so that a greater understanding of their life history and ecology can be obtained.

MATERIALS, METHODS, AND TERMS

Taxonomic Materials

Material examined in the course of this study included 1025 adults specimens of *Abaris* and *Neotalus* species. A number of these were examined in detail including dissection of various internal systems. Material was taken on loan from collections listed below. Museum codens are used in the text and the names listed here are the individuals I corresponded with to obtain material and/or those who processed the loans for me.

Museums and Codens.—AMNH: Department of Entomology, American Museum of Natural History, New York, New York (L. H. Herman).

BMNH: Department of Entomology, British Museum, London (Natural History) (S. Hine).

BORD: C. Bordon collection, Maracay, Venezuela (C. Bordon).

BPBM: Bishop Museum, Honolulu, Hawaii (G. A. Samuelson).

CASC: Department of Entomology, California Academy of Sciences, San Francisco, California (D. H. Kavanaugh, R. Brett).

CMNC: Entomology, Canadian Museum of Nature, Ottawa, Ontario.

CMNH: Section of Invertebrate Zoology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (R. L. Davidson).

CNCI: Canadian National Collection, Biosystematics Research Institute, Agriculture and Agri-Food Canada, Ottawa, Canada (Y. Bousquet).

CUIC: Department of Entomology, Cornell University, Ithaca, New York (J. K. Liebherr).

EMEC: Essig Museum of Entomology, Berkeley, University of California, Berkeley, California (C. Barr).

INBC: Instituto Nacional de Biodiversidad (INBio), Costa Rica, Santo Domingo de Heredia.

IZWP: Instytut Zoologii, Polska Akademia Nauk, Warszawa, Poland (T. Huflejt).

KWWC: Kipling Will Collection, Berkeley, California.

MSNM: Museo di Storia Naturale di Milano, Milan, Italy (M. Pavesi, C. Leonardi).

MCZC: Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (P. Perkins).

MHNP: Entomologie, Museum National d'Histoire Naturelle, Paris, France (T. Deuve).

MIZA: Museo del Instituto de Zoología Agrícola Francisco Fernández Yépez, Maracay, Venezuela (L. Joly, J. Clavio).

MNHB: Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany.

NMW: Zweite Zoologische Abteilung, Naturhistorisches Museum Wien, Wien, Austria (H. Schonmann, E. Kirschenhofer).

OSUC: Department of Entomology, Ohio State University, Columbus, Ohio (N. Johnson).

QCAZ: Catholic Zoology Museum, Pontificia Universidad Catolica del Ecuador, Quito, Ecuador (G. Onore).

RSCI: Riccardo Sciaky Collection, Milan, Italy.

SEMC: Snow Entomological Division, The Natural History Museum of the University of Kansas, Lawrence, Kansas (R. Brooks, J. S. Ashe).

STOC: H. Stockwell Collection.

UASM: Strickland Museum, Dept. of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada (D. Shpeley, G. E. Ball).

UATU: Department of Entomology, University of Arizona, Tucson, Arizona (C. A. Olson, D. R. Maddison).

UMMZ: University of Michigan, Museum of Zoology, Ann Arbor, Michigan (M. O'Brien).

UVGC: Universidad del Valle de Guatemala, Guatemala City (J. Schuster).

USNM: Department of Entomology, United States National Museum of Natural History, Smithsonian Institution (T. L. Erwin, D. Furth)

Taxonomic Methods

Species Recognition.—Species were recognized by a set of defining characteristics that permit grouping like individuals from other such individuals with a different set of characteristics. This is essentially the species definition of Nixon and Wheeler (1990).

When multiple specimens were available, variation in characteristics for the species could be assessed and the limits of the defining characters understood. However, when only a single, notably different specimen is available it was necessary to decide if the difference was of specific value. For species based on one or very few specimens, I relied on characters that seemed to be beyond individual variation observed in species known from larger samples. In general these unique specimens were not dissected, so external characteristics that were found to be correlated with genitalic differences in better represented species were relied on. In a few cases a specimen was included within my interpretation of a species, though not in the type series, because it exhibited slight differences that may ultimately prove to define it as a member of a distinct species. I felt it was best not to multiply names in these marginal cases until more material is collected, permitting a robust test of stability of species definitions based on observed character differences.

Species of these genera, like nearly all of life, do not have any single characteristic or complex of characteristics that we can examine to inform us with certainty on their reproductive isolation, or any other possible mode of speciation. Entities named here may be explained, after they are recognized, as real biological and evolutionary individuals. But regardless whether the process thought to underlie species generation is correct or not, species recognition remains the same as it has for all of recorded history, based on empirical observation of characteristics augmented by knowledge of reproduction and development in the rare cases where those data are known. Of course, hypotheses may be adjusted, if necessary, in light of observations of reproductive isolation or interbreeding.

Ranking Criteria and Classification.—No general standard exists for recognizing supraspecific groups in pterostichine ground beetles. The repeated failure to support a monophyletic Pterostichini (*auctorum*) demonstrates that this taxon is a grade (Will, 2000). My use of the term *pterostichine grade* emphasizes the lack of monophyly among the presently included taxa.

The Holarctic pterostichine grade fauna, primarily *Pterostichus* Bonelli, 1810,

is superficially rather uniform in appearance and some recent authors have separated supraspecific groups by very small character differences. The application of similar criteria to the South American and Australian taxa has resulted in what I feel is an extreme emphasis on differences with less regard for grouping similarities. This has led to the recognition of too many supraspecific taxa. With this in mind I have attempted to minimize the number of formal names (genera and subgenera) proposed here, but have named clades (species-groups) that, based on the characters, seem to represent biologically interesting groups and groups of similar form. These names are provided for biologists who may need to discuss the ecology, behavior, etc., of a monophyletic group. When the higher elements of the pterostichine grade are established, some clades (genus-groups) may come to have a formal position in the Linnaean hierarchy.

It is neither practical nor desirable to have a name affixed to every branching point of the cladogram. The classification here is completely consistent with the phylogenetic hypothesis but is not identical to it. These two constructs, cladogram and classification, have slightly different but interconnected purposes. The former provides a complete summary of characters and relationships, and is the basis for discussion of hypotheses of common descent. The latter is the primary means of information retrieval for the taxa, and so should be a useful mnemonic device. In order to fulfill this function, the classification necessarily ignores some of the details of the cladogram and focuses on the aspects deemed likely to be biologically important.

I use the term *sedis mutabilis* as proposed by Wiley (1979; 1981) for the polytomous relationship of basal Abaridius species.

Phylogeny Reconstruction.—The matrix was constructed with the computer program WinClada (Nixon, 1999) and submitted to NONA (Goloboff, 1994) for analysis. NONA's default settings were used for a heuristic search for most parsimonious trees (see NONA documentation). The search was done by submitting the matrix via WinClada using number of replications = 100 (Mult*100), starting trees per replication = 15 (hold/15), random seed = Time (rs0) and the search strategy was multiple TBR+TBR (mult*100; Max*). Aspects of cladistic methods and subsequent interpretation of the pattern as a phylogenetic hypothesis employed here are discussed in my analysis of the genus *Lophoglossus* LeConte, 1852 (Will, 1999).

Preparation and Imaging Techniques.—External structures were examined using a dissecting stereo-microscope at magnification of 100× or less. Some smaller structures and microsculpture of legs, mouthparts, and elytra were examined and photographed using a Hitachi 4500 scanning electron microscope. Disarticulated cuticular structures, including all external parts of the body and various internal systems, were cleared in 10% KOH and mounted on glycerine slides, then examined using a phase-contrast compound microscope.

Methods generally used for preparation of male genitalia follow Allen (1972). However, the small size of most species did not allow for the successful eversion of the endophallus using Allen's methods. Two alternatives were tried with some success for each. First fluid pressure was applied to the foramen using the Phalloblaster machine (vesica everter, Matthews, 1998) for *Neotalus portai* (Straneo). The small size of *Abaris* specimens precluded the use of this machine as the needle diameter exceeds the diameter of the median lobe. Instead of direct fluid pressure, a rapid change in osmotic pressure was used to evert the endophallus in some species. The median lobe was softened in KOH and then dehydrated in 95% EtOH. In order to

increase pressure pushing out the endophallus, a small drop of water soluble glue was placed on the foramen to prevent equalization through the foramen. When the dehydrated median lobe was placed in distilled water, pressure from the flow of water into the lobe via the gonopore forced out the endophallus.

Preparation of female reproductive tracts and genitalia followed procedures outlined by Liebherr and Will (1998).

Initially, drawings were made as pencil line-drawings using an ocular grid or camera lucida. These line drawings were digitized using a flatbed scanner, "inked" and shaded on a personal computer using the Corel Photo-Paint™ version 7.467.

Some cases digital images of whole or slide-mounted portions of specimens were captured using a video microscope and a Snappy Video grabber version 3.0 connected to a personal computer. These images were enhanced in Corel Photo-Paint™ version 7.467 and either printed from a desktop printer or black and white print film.

Locality Information.—Locality information is provided for each species and is divided between type and non-type information. Data from type specimens that are verbatim from the labels are enclosed in double quotation marks with the description of the kind of label and a note if handwritten. Notes not on the specimen labels and the description of the labels are added for clarity and this information placed between square brackets ([. . .]). Unless otherwise noted, labels are white, rectangular with black ink. In as much detail as could be clearly confirmed locality data for other material examined is listed for each species by country in descending order from largest political unit to smallest site information, including latitude and longitude. Altitude and seasonal information are summarized in the section "Notes on Life History" and are listed under each species if any additional data were available beyond that found on the type specimens.

Maps show the location of collections for each of the species either from specimen data labels or from published records. A symbol on the map primarily represents a single collecting site. Multiple sites are represented by a single symbol in cases where collecting sites are very close and multiple symbols on the map would be impossible to discern or be confusing. If label data were unclear or the locality not definitively identifiable, the data are listed but not plotted on the map. In cases where this was the only record for a country a symbol was place on the map with a "?" to identify it as a questionable record.

Terms

Measurements.—*Overall length* was measured using an ocular reticle and generally was the entire distance from the base of the labrum to the tip of the left elytron. In specimens where it was not possible to measure this way accurately because of the head position, length was standardized using the sum of lengths: 1. base of labrum to the cervical collar, 2. apex to base of pronotum along the midline, 3. base of scutellum to apex of left elytron.

The *ratio of elytral interval widths* is the width of interval 3 divided by the width of interval 2. Measurements were taken by placing an ocular reticle across the intervals at the level of the dorsal setigerous puncture.

Ocular ratio is a measurement of the relative size of the eyes or "bug eyedness" of the beetles. This ratio is the width over the widest point of the eyes divided by the width between the eyes at the level of the anterior supraorbital setae.

Body Parts.—Terms for adult external structures and segmentation follow

Lawrence and Britton (1994). One exception is the use of sterna II–VII for normally exposed ventral abdominal segments rather than sternites II–VII as used by Lawrence and Britton. This follows the definition of sternum as a single ventral division per segment, as is found in adult beetles, and sternites as subdivisions of a sternum as is found in many larvae (Snodgrass, 1935; Torre-Bueno, 1937).

Terms for the female reproductive tract and external genital structures follow Liebherr and Will (1998). Nomenclature of endophallic structures follows Noonan (1991).

The median lobe of the aedeagus is discussed using the following: basal bulb, generally expanded region of the foramen from the base to the parameres; blade, remaining section from the basal bulb to the tip; apex, apical portion of blade from the level of the ostium to the tip; and tip, portion of the apex of the median lobe beyond the ostium. Terms used for colors follow Torre-Bueno (1937).

The term scutellar stria has been used to refer to the short striae on the elytra near the scutellum even though they may not be homologous structures across all groups. The term has been used in reference to the parascutellar striae, which are directly adjacent to the scutellum and continuous with the basal marginal border of the elytra when the border is evident and striae are sulciform. Additionally, the term has been used for the short basal section of stria 1 when that stria is interrupted, even though this section is not adjacent to the scutellum. In order to be consistent with my hypotheses of primary homology I abandon the term scutellar stria but retain the use of *parascutellar stria* as restricted above. In all abariform taxa elytral stria 1 is continuous with the parascutellar stria. Stria 1 may end at its junction with the parascutellar stria or have a short, disconnected basal section arising from near the basal setigerous puncture. When stria 1 is interrupted and the disconnected basal section is present, it is referred to as the *basal section of stria 1*.

Discussion of Clades and Taxa.—Cladistic diagnoses are summaries of synapomorphic characteristics of a monophyletic group of taxa based on the cladogram present herein. The purpose of this section is to allow for quick assessment of group membership. The character states of a clade that apply to all included taxa, are not discussed in subordinate clades as they are plesiomorphic and are not useful for assessing group membership at that level.

Recognitory diagnoses correspond to the more traditional diagnosis found in most taxonomic works. The characteristics provided under this heading are intended to permit accurate recognition of specimens. This includes any general attributes and comparative aspects, without regard to phylogenetic implications of the characteristic.

TAXONOMIC AND CLADISTIC ACCOUNTS

Systematic Entomology
Order Coleoptera
Family Carabidae
Subfamily Harpalinae
Tribe Pterostichini (Auctorum)

KEY TO ADULT *NEOTALUS* NEW GENUS AND *ABARIS* DEJEAN SPECIES

1. Metacoxal anterior sulcus incomplete, ended medially on coxa, broadly arcuate in most species, not approaching anterior margin (Fig. 3A); basal section of stria 1 present or absent 2

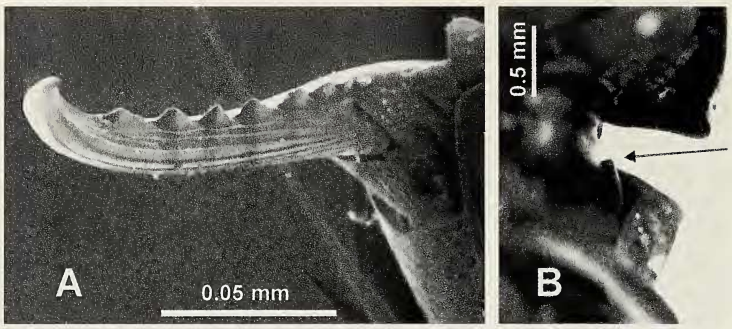

Fig. 2.—Structures of abariform species. A. Scanning electron micrograph, pro tarsal claw of *Abaris aenea* Dejean showing pectination. B. Digitized video-capture image, ventral view, pro and mesothoracic area, *Neotalus portai* (Straneo), mesepimeral tubercle indicated by arrow.

1′. Metacoxal anterior sulcus complete, ended at or near apex, straight, not broadly arcuate, approaching anterior coxal margin, (Fig. 3B); basal section of stria 1 absent. *Abaris tachypoides*-group 21

2 (1). Basal section of stria 1 absent 3
2′. Basal section of stria 1 present 8

3 (2). Sterna V–VII without sulci (Fig. 4C); tarsal claws pectinate (Fig. 2A) 4
3′. Sterna V–VII with sulci (Fig. 4A); tarsal claws smooth . . . . . *Neotalus portai* (Straneo)

4 (3). Pronotum widest just before middle, lateral margin reflexed in basal third or not; most species shinier with faint or obsolete microsculpture; if microsculpture obvious, then pronotum in basal third laterally distinctly reflexed (Fig. 24D–E) 5
4′. Pronotum widest slightly behind middle, lateral margin not reflexed in basal third (Fig. 25D); dull species, microlines forming reticulate microsculpture obvious. Argentina . . . . . [12] *Abaris basistriata* Chaudoir (in part)

5 (4). Microsculpture faint but visible on head and pronotum 6
5′. Microsculpture obsolete on head and pronotum . . . . . [4] *Abaris aenea* Dejean

6 (5). Elytral interval 3 much broader than 2; width ratio 3/2 > 1.4 7
6′. Elytral interval 3 only slightly wider than 2; width ratio 3/2 < 1.4 . . . . . [5] *Abaris erwini* new species

7 (6). Pronotum punctate basally and laterally, base laterally sinuate with median base distinctly extended posterad of hind angles (Fig. 24H) South America . . . . . [7] *Abaris notiophiloides* Bates
7′. Pronotum impunctate laterally, base in some with a few shallow punctulae, base not

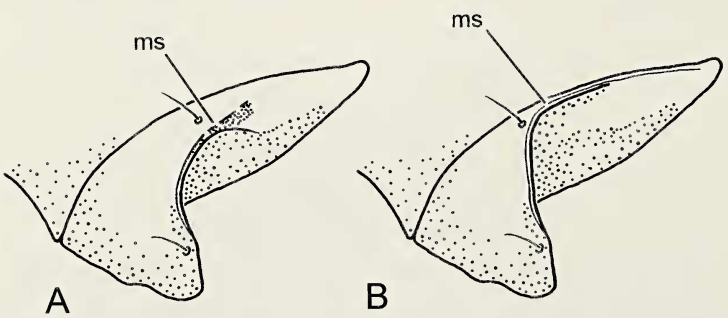

Fig. 3.—Line drawing illustrating diagrammatically abariform left metacoxae. A. With incomplete/arcuate metacoxal anterior sulcus (ms). B. With straight/appressed metacoxal anterior sulcus (ms).

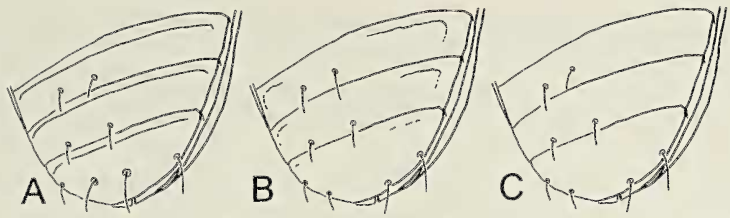

Fig. 4.—Line drawing illustrating diagrammatically abariform abdominal sterna. A. With complete transverse sulci. B. Incomplete/laterally present sulci. C. Sulci absent.

sinuate; hind angles only slightly anterior to median base (Fig. 24G) Central America/ Mexico . . . . . [6] *Abaris aquilonaria* new species

8 (2′). Sterna V–VII with lateral sulci, medially complete or interrupted (Fig. 4A–B); sulci shallowly to deeply impressed, best developed on sternum VI (variable species handled in both halves of couplet) 9

8′. Sterna V–VII without a trace of lateral or medial sulci (Fig. 4C) 19

9 (8). Sulci on sterna V–VII complete (Fig. 4A) 10

9′. Sulci on sterna V–VII broadly interrupted medially and slightly developed laterally (Fig. 4B) 12

10 (9). Pronotum constricted at base, widest in anterior half; both basal foveae distinct . . . 11

10′. Pronotum widest at base; outer basal foveae absent (Fig. 25E) . . . . . [13] *Abaris metallica* new species

11 (10). Dorsum of head and pronotum metallic green, elytra cupreous; lateral pronotal margins sinuate to base, hind angles clearly denticulate (Fig. 25F) . . . . . [14] *Abaris bicolor* new species

11′. Entire dorsum cupreous; lateral pronotal margins convexly arcuate to base, hind angles minutely denticulate (Fig. 25G) . . . . . [15] *Abaris nobilis* new species

12 (9′). Disc of pronotum shiny, without obvious microsculpture 13

12′. Disc of pronotum dull, with obvious mesh microsculpture either reticulate or somewhat transversely elongate 18

13 (12). Pronotal lateral margin sinuate anterior of hind angles, reflexed in basal third (Fig. 24A–B); narrowly convex immediately lateral of basal fovea 14

13′. Pronotal margin laterally arcuate and straight or subsinuate anterior of hind angles, not reflexed laterally; convex from basal fovea to lateral margin. (Fig. 25B–C) 17

14 (13). Pronotum with outer basal foveae present, punctate or rugose along base and/or punctulate in foveae (Fig. 24A–B) 16

14′. Pronotum with outer foveae absent, impunctate (Fig. 24C) 15

15 (14). Median lobe tip asymmetrical in dorsal view, left edge emarginate (Fig. 21E) . . . . . *Abaris striolata* Bates (in part).

15′. Median lobe tip nearly symmetrical in dorsal view, left edge convex (Fig. 21G) . . . . . [3] *Abaris robustula* Tschitschérine

16 (14). Pronotal base distinctly rugose medially and around basal foveae; aedeagus median lobe tip very broad in dorsal view (Fig. 21A–C) . . . . [1] *Abaris napoensis* new species

16′. Pronotal base impunctate or faintly punctured medially and around basal foveae; aedeagus median lobe tip acuminate in dorsal view (Fig. 21D–E) . . . . . [2] *Abaris striolata* Bates (in part)

17 (13′). Pronotal base impunctate (Fig. 25C); endophallus of aedeagus without spine patch visible at bend of median lobe (Fig. 23D); spermathecal duct tightly twisted . . . . . [11] *Abaris mina* new species

17′. Pronotal base punctate (Fig. 25B); endophallus of aedeagus with spine patch visible at bend of median lobe (Fig. 23A); spermathecal duct broad, not twisted (Fig. 19E) . . . . . [10] *Abaris picipes* Bates

18 (12′). Pronotal base with coarse punctulae in basal foveae (Fig. 25A); dorsum black; obvious reticulate microsculpture on pronotum, transversely elongate mesh on elytra, elytra shiny. Mexico . . . . . [9] *Abaris bigenera* Bates

18′. Pronotal base without coarse punctulae (Fig. 24I); dorsum aeneous; reticulate microsculpture obvious throughout, dull species. South America . . . . . [8] *Abaris impunctata* new species

19 (8′). Pronotal lateral margins not reflexed, arcuate, straight just anterior to slightly obtuse hind angles (Fig. 25B–D) 20

19′. Pronotal lateral margins distinctly reflexed basally and subsinuate to right angled hind angles (Fig. 24B) . . . . . [2] *Abaris striolata* Bates (in part)

20 (19). Reticulate microsculpture obvious on head and pronotum; dorsal surface duller . . . . . [12] *Abaris basistriata* Chaudoir

20′. Microsculpture obsolete on head and pronotum; dorsal surface very shiny . . . . . [10] *Abaris picipes* Bates

21 (1′). Sterna V–VII with lateral sulci, medially complete or interrupted (Fig. 4A–B) 22

21′. Sterna V–VII without sulci (Fig. 4C) 25

22 (21). Pronotal base without punctulae; if punctulae present then outer basal foveae clearly round (Fig. 26A) . . . . . [17] *Abaris franiai* new species

22′. Pronotal base with coarse punctulae; outer basal foveae elongate 23

23 (22′). Apex of pronotum wider, tip of front angles distant from occiput and slightly produced (Fig. 25H, 26B) 24

23′. Apex of pronotum narrow, tightly rounded and appressed to occiput, front angles not produced (Fig. 9) . . . . . [19] *Abaris tachypoides* Bates

24 (23). Pronotum medially punctate between inner foveae (Fig. 25H); mental tooth broadly flattened at apex . . . . . [16] *Abaris nitida* new species

24′. Pronotum medially impunctate between inner foveae (Fig. 26B); mental tooth rounded at apex . . . . . [18] *Abaris inflata* new species

25 (21′). Pronotum relatively small, lateral margins sinuate and narrowly constricted basally (Fig. 26D–E); width of pronotum at base less than width across eyes, or if approximately equal then legs bicolored 25

25′. Pronotum relatively larger, lateral margins sinuate or not; width of base greater than or equal to width across eyes, legs not distinctly bicolored 26

26 (25). Coxae, trochanters and base of femora darkly infuscated, contrasted with flavous apices of femora, tibiae and tarsi; dorsum black; pronotal base punctulate; front angles of pronotum slightly produced (Fig. 26D) . . . . . [21] *Abaris nigra* new species

26′. Legs concolorous, flavous; dorsum bronzed; pronotal base smooth, only foveae impressed; front angles of pronotum round and tightly appressed to occiput (Fig. 26E) . . . . . [22] *Abaris inaequaloides* new species

27 (25′). Pronotal base with irregular, coarse punctulae at least in area of basal fovea; if punctulae restricted to fovea then head dull from reticulate microsculpture 28

27′. Pronotal base without punctulae or with only a few shallow punctulae in basal fovea; if punctulae present then head quite shiny, micro-lines scarcely visible 29

28 (27). Mental tooth form simple, sagittiform . . . . . [25] *Abaris wardi* new species

28′. Mental tooth apex blunt and slightly emarginate . . . . . [23] *Abaris opaca* new species

29 (27′). Elytral intervals convex, more prominently so in apical third; eastern and southern Mexico, Central or South America 30

29′. Elytral intervals flat throughout their length; northwestern Mexico, Baja California, Arizona, southern California . . . . . [24] *Abaris splendidula* (LeConte)

30 (29). Dorsum uniformly shinier, though not brilliantly so, microsculpture of pronotal disc transverse, somewhat irregular mesh, transverse mesh on elytra. Central America, Mexico . . . . . [26] *Abaris aequinoctialis* Chaudoir

30′. Pronotal disc very dull from reticulate microsculpture; elytral microsculpture reticulate, shinier than pronotal disc. South America 31

31 (30′). Pronotal base not bordered laterally (Fig. 26C) . . . . . [20] *Abaris convexa* new species

31′. Pronotal base with distinct lateral border (Fig. 27C) . . . . [27]*Abaris retiaria* new species

Classification and Checklist of Abariform Genera, Subgenera and Species

(*Pseudabarys* (*Neotalus* + *Abaris*))
Neotalus Will, new genus (one species)
Neotalus portai (Straneo)
Abaris Dejean (27 species)
Abaris sensu stricto
[*A. striolata*-group]
1. *A. napoensis* Will, new species
2. *A. striolata* Bates
[*A. aenea*-group]
3. *A. robustula* Tschitschérine
4. *A. aenea* Dejean
5. *A. erwini* Will, new species
6. *A. aquilonaria* Will, new species
7. *A. notiophiloides* Bates
[*A. picipes*-group]
8. *A. impunctata* Will, new species
9. *A. bigenera* Bates
10. *A. picipes* Bates
11. *A. mina* Will, new species
12. *A. basistriata* Chaudoir
13. *A. metallica* Will, new species
Abaridius Chaudoir
[*sedis mutabilis*]
14. *A. bicolor* Will, new species
15. *A. nobilis* Will, new species
[*A. tachypoides*-group]
16. *A. nitida* Will, new species
17. *A. franiai* Will, new species
18. *A. inflata* Will, new species
19. *A. tachypoides* Bates
20. *A. convexa* Will, new species
21. *A. nigra* Will, new species
22. *A. inaequaloides* Will, new species
23. *A. opaca* Will, new species
24. *A. splendidula* (LeConte)
25. *A. wardi* Will, new species
26. *A. aequinoctialis* Chaudoir
27. *A. retiaria* Will, new species

Accounts of Clades

*Abariform Clade (Pseudabarys (*Neotalus + Abaris*))*

Cladistic Diagnosis.—All members of the abariform clade share the following non-homoplasious synapomorphies (Fig. 31: characters 2, 8, 12, 26): eyes large, ocular ratio greater than 1.60; humeral umbilicate puncture 2 displaced medially from 1 and 3; ventral setae of tarsomere 5 of unequal length and paired; dorsal bursal glands present (Fig. 5A–B).

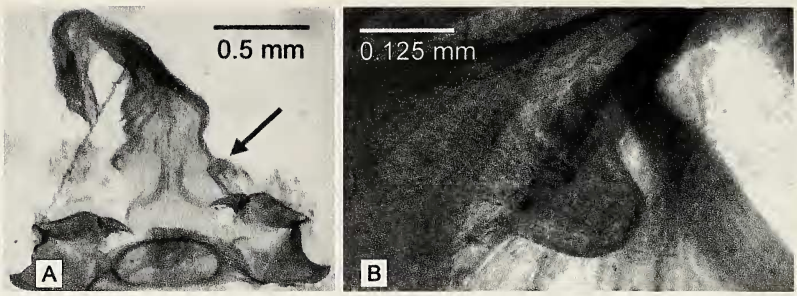

Fig. 5.—*Abaris aenea* Dejean digitized video-capture images of female reproductive tract, showing paired dorsal glands. A. Ventral view of bursa laid flat, arrow indicates gland. B. Single gland enlarged.

Clade (Neotalus + Abaris)

Cladistic Diagnosis.—All members of this clade share the following synapomorphies (Fig. 31: characters 1, 25): maxillary palpomere 3 much smaller than palpomere 4 (Fig. 28B), diverticulum of the spermatheca appended gland absent.

Neotalus, **new genus**

Type Species.—Bothynoproctus portai Straneo; here designated.

Etymology of Generic Name.—Noun in apposition, masculine. *Neotalus* is a genus-group name formed from the Greek neos (νεοσ)—new and Talos (Ταλοσ)—the name of the bronze giant faced by the Argonauts in Crete. The single New World species placed in this genus is larger than species in the genus *Abaris*, has a distinctive metallic luster and lacks the pectinate claws found in *Abaris* species.

Nomenclatural and Taxonomic Notes.—Straneo (1941) described *Bothynoproctus portai* placing it with *B. mattoensis* Tschitschérine, 1900, the type species for the genus. No doubt as a result of World War II, Stefano Straneo did not have the benefit of seeing the type of *B. mattoensis*, and therefore he misplaced his new species. The characteristic deep punctures of the submentum and sternum VII in *B. mattoensis* are lacking in *N. portai*. The former is not closely related to the abariform genera and is more closely related to *Dyschromus* Chaudoir and *Tichonilla* Strand, 1942 (Will, 2000), whereas the latter has several significant synapomorphies in common with *Abaris* species.

Based on these characteristics and my analysis of a broader set of characters (Will, 2000), Straneo's species is removed from *Bothynoproctus* and a new genus, *Neotalus*, is proposed to hold this species. Therefore, *Neotalus portai* (Straneo) is the type species for this monotypic genus.

Cladistic Diagnosis.—As this is a monotypic genus, its synapomorphic characters cannot be specified. If a second species is found that groups with *N. portai* it will likely share some of the apomorphic characteristics described for the species below.

Recognitory Diagnosis of Adults.—See species below and characters in the key.

Description of Adults.—None required because the genus is monotypic. Its characters are as in the type species described below.

Distribution.—See species account below and figure 10.

Fig. 6.—Dorsal habitus of *Neotalus portai* (Straneo).

Species Account

Neotalus portai (Straneo, 1941), **new combination**
Fig. 2B, 6, 10

Bothynoproctus portai Straneo, 1941:28.

Type Material.—HOLOTYPE. Female. Labeled: "Forét Vierge, au bord de Riv. Paraguay, S Antonio" [handwritten]/"Holotypus portai" [red label]/"portai Stran." [handwritten, red ink], [MSNM]. ALLOTYPE. Male, labeled: "S.Antonio" [handwritten], "Allotypus" [red label]/[dissected genitalia and mouthparts glued to card] [MSNM]. PARATYPES. 2 Males, same data as Allotype, both labeled with "M.C.Z. Paratype 28422", MCZC.

Type Locality.—Paraguay, S Antonio, Staz. Entomol. Fabre., from original description.

Range.—Bolivia, Brazil, Paraguay (Fig. 10)

Recognitory Diagnosis of Adults.—Recognized from all other Carabidae by the combination of form of mouthparts—labial palpi short and broad, lacinia large with a thick, curved apical digitus, maxillary palpi broadly fusiform—and mesepisterna with large tubercle (Fig. 2B) and a corresponding protuberance of pronotal base, tarsal claws smooth, and female reproductive tract with paired bursal glands (Fig. 5A–B).

Description.—In addition to characteristics of the *Neotalus* + *Abaris* clade, large sized, 7.0–8.5 mm. Elytra aeneous or cupreous to vinous, head and pronotum darker, shiny. Ventral surface black, tarsi and palpi paler brunneous.

Head. Large, very broad, frontal impressions deep, divergent. Fronto-clypeal suture impressed, clypeus emarginate, membrane at base of labrum exposed. Eyes very large and prominent, hemispherical, ocular ratio 1.62–1.72. Submentum separated from mentum by distinct suture. Mentum very broad, with epilobes slightly produced beyond broad, apically emarginate medial tooth. Ligula with glossal sclerite broad and convexly rounded at apex with two large setae. Paraglossae very long and free with cristate microspicules, especially laterally and near apex. Labial palpi short and broad, palpomere 2 with two large medial setae and 2–3 small apical setae, palpomere 3 with small scattered setae. Maxillae with lacinia large and with a thick, curved apical digitus plus a medial field of large spines with scattered finer setae. Cardo distinctly developed, stipes with two large setae, one apical one basal. Palpifer simple, maxillary palpi fusiform but broad; palpomere 1 broad with a few small setae at apex, palpomere 3 very short relative to palpomere 4 and with several small setae at its apex, palpomere 4 expanded at tip with scattered small setae, 2–3 lateral setae larger. Galea with two small terminal setae. Mandibles with retinaculum discrete, premolar and molar teeth small.

Thorax. Ventral thoracic segments impunctate and moderately shiny, microsculpture faint mesh. Pronotum broad, lateral margins straight before hind angles, apical margin straight, front angles very slightly produced, basal margin straight, inner basal foveae present, broadly impressed, outer basal foveae shallow round depressions. Prosternal process apically margined. Metepisternum quadrate. Flight wings small scales. Elytra broad, depressed, oblong-ovate, humeri angulate, equal to width of pronotal base, striae deep, smooth (Fig. 6); stria 1 continuous with parascutellar stria, basal section of stria 1 absent, elytral intervals slightly convex; each elytron with a single setigerous dorsal puncture in apical half of third interval; second and third intervals of approximately equal width. Legs of moderate length; metacoxal anterior sulcus divergent, and arcuately ended medially in coxa, coxae each with two large setae; pro and meso-trochanters each with a single large seta, metatrochanter apically rounded without setae; femora slender, setation as follows: profemora—anterior face, 1 apical, 1 medial; dorsal face, 1 apical and 2 subapical; posterior face, 1 apical, 1 medial and 1 basal; mesofemora—anterior face, 1 apical, 1 medial and 1 basal; dorsal face with row of 4 setae, 2–4 apical; posterior face, 0–2 setae and occasional scattered setae laterally; metafemora—anterior face, 1 apical, 1 medial; dorsal face with row of 2–4 setae; posterior face glabrous. Tibiae slender; protibia with a row of 3–4 fine setae on medial face and a row of 3–5 coarser setae laterally, two clip setae, anterior brush of fine setae ends at enlarged medial seta; meso- and metatibiae with four rows of prominent setae, medial row very fine, others much stouter. Male protarsomeres expanded, first to third with articulo-setae ventrally (Stork, 1980). Four basal protarsomeres of female and four basal meso- and metatarsomeres in both sexes with two, more or less distinctly defined rows of ventral setae and numerous scattered setae, most scattered setae smaller than the row setae. Fifth tarsomere with two pairs of fine ventral setae, apical nearly twice length of subapical. Tarsal claws smooth.

Abdomen. Sterna moderately shiny, microsculpture obscure. Transverse sulcus of sterna V–VII present and entire. Male genitalia simple, endophallus minutely spinose and scrotiform. Median lobe of aedeagus straight, smooth. Female reproductive tract with spermatheca not discrete from duct, duct broad. Gonocoxite-1 with 3 small ensiform setae near apex, gonocoxite-2 arcuate and laterally excavated, apex round, 1 dorsal and 1 lateral large ensiform seta, 2 nematiform setae in elongate furrow. Paired bursal glands dorsally present.

Additional character information is provided in original description.

Notes on Life History.—The only information beyond data given for the types is on a specimen from Sará, Bolivia, collected at 450 m in November.

Material Examined.—Twelve specimens, including the type series, were examined. Nontype material from: **BOLIVIA. La Paz:** Sud. Yungas. Ocbaya [MSNM]. **Sará:** [CMNH, MNHB].
BRAZIL. Chapada [CMNH].
PARAGUAY. Central: [MHNP].
UNKNOWN: [MSNM].

Genus *Abaris* Dejean, 1831

Abaris Dejean, 1831:780. TYPE SPECIES (by monotypy): *Abaris aenea* Dejean, 1831:781. Dejean and Boisduval, 1832:211. Laporte, 1840:118. Chaudoir, 1852:76–77. Chenu, 1851:161. Lacordaire, 1854:347. Bates, 1871:218–220. Bates, 1882:85. Csiki, 1930:576. Straneo, 1939:38. Blackwelder, 1944:35. Reichardt, 1977:409. Straneo, 1977:111,115. Straneo, 1979:350,352. Bousquet, 1984:384–389. Bousquet and Larochelle, 1993:165. Bousquet and Liebherr, 1994:435–441. Lorenz, 1998:243. Bousquet, 1999:48–51. Ball and Bousquet, 2001:85.

Abarys Agassiz, 1846:1 (unjustified emendation). Gemminger and Harold, 1868:366. Chaudoir, 1873: 96. Tschitschérine, 1898:83.

Abaridius Chaudoir, 1873:97. Reichardt, 1977:409. Erwin, 1991:40. **New Synonymy:** Type species (original designation): *Abaris tachypoides* Bates, 1871:220.

Etymology.—Dejean constructed the generic name from the Greek using α, absence of, and βαρυσ, heavy, in reference to the lightly constructed form and fleetness of foot for the included species. Dejean transcribed βαρυσ with υ = i. Most Greek lexicons transcribe υ = y, which led to the unjustified emendation of *Abaris* by Agassiz (1846) to *Abarys*. Indeed, a strict transcription of *Abaris* back to the Greek would mean "not boat shaped," whereas *abarys* would translate to "not heavy" as described by Dejean. Nonetheless, the ICZN (1999, Art. 33.2.3) does not allow emendation of a name based on changes in character transcription.

Abarys (αβαρυσ) is a masculine word in Greek, but *Abaris* as used by Dejean is a feminine form. He did this in conjunction with the single species he named *aenea*, which is clearly feminine. Therefore, various specific epithets that have been changed to, or originally formed in the masculine must be made to agree in gender with *Abaris* as a feminine Latinized noun.

Synonymy.—Bates (1871) described five *Abaris* species. These plus *A. aequinoctialis* described by Chaudoir (1852) increased the total number of *Abaris* species to seven. Bates does not mention the presence of pectinate tarsal claws in his discussion of the characteristics of the genus, but does note the transverse sulci on the sterna of some species. Chaudoir (1873) subsequently newly defined two genera, *Abaridius* and *Pseudabarys* that included two of Bates' species, *A. tachypoides* and *A. robustus*, respectively. The three genera were diagnosed as follows: *Abaris* species with pectinate claws and smooth sterna, *Abaridius* species with both pectinate claws and ventral sulci, and *Pseudabarys* with smooth claws and a sulcate venter. My study of these characteristics and additional characters shows that *Abaris* and *Abaridius* are congeneric. *Abaris* is distinct from *Pseudabarys*, but the latter is in need of revision and its monophyly has not been tested.

Cladistic Diagnosis.—*Abaris* is considered a monophyletic group within the larger abariform clade and is defined by the synapomorphous presence of pectinate claws (Fig. 2, Fig. 31: character 11).

Recognitory Diagnosis.—Recognized from all other Carabidae by the combination of pectinate claws, distinctly developed internal and external elytral plica (sensu Liebherr, 1986:90–91) and paired bursal glands in the female reproductive tract (Fig. 5).

Description of Adults.—In addition to characteristics of the *Neotalus* + *Abaris* clade, small to medium sized ground beetles, 4.8–8.9 mm. Nearly all individuals with an aeneous or virescent luster, sometimes brilliantly so (only *A. nigra* and some individuals of *A. bigenera* black without metallic luster). Nearly all individuals shiny or very shiny. Body ventrally piceous, rufous or ferruginous, legs and mouthparts paler than venter in most, some individuals variously infuscated.

Head. Head large, relatively broad. Frontal impressions present, deep in most species, shallowest in members of the *A. picipes*-group. Eyes very large and prominent, hemispherical, ocular ratio 1.63–

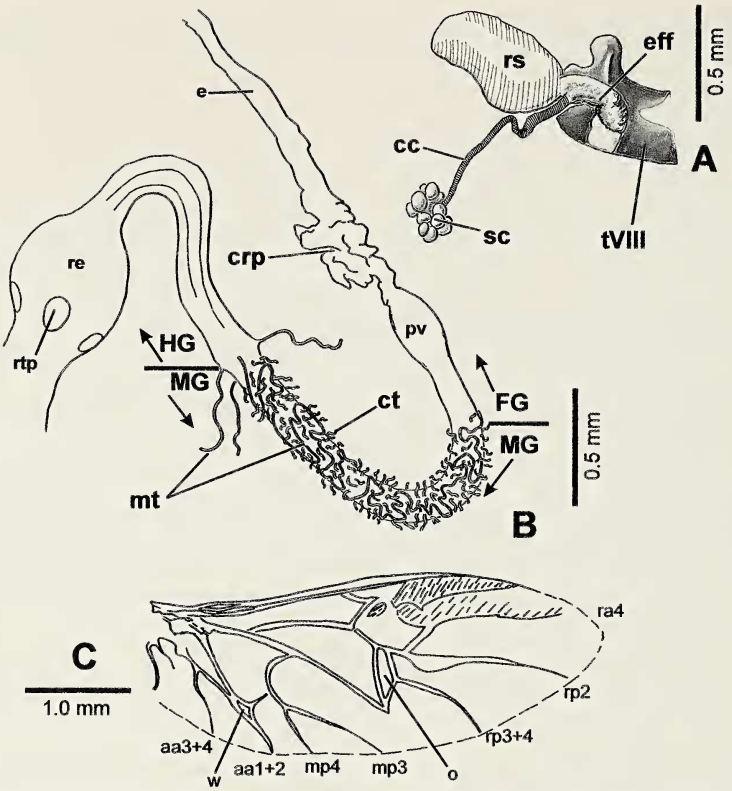

Fig. 7.—Structures of *Abaris splendidula* (LeConte). A. Pygidial gland system, ventral view of right gland. B. Extracted gut. C. Right hind wing, dorsal view. Legend: aa1+2, anterior anal vein 1+2; aa3+4, anterior anal vein 3+4; cc, collecting canal; crp, crop; ct, crypt ; e, esophagus; eff, efferent duct; FG, foregut; HG, hindgut; MG, midgut; mt, Malpigian tubles; mp3, posterior medial vein 3; mp4, posterior medial vein 4; o, oblongum cell; pv, proventriculus; ra4, anterior radial vein 4; re, rectum; rp2, posterior radial vein 2; rp3+4, posterior radial vein 3+4; rs, gland reservoir; rtp, rectal pad; sc, secretory cells; tVIII, tergite VIII.

1.91, most greater than 1.70, eyes least developed in *A. nobilis*. Submentum separated from mentum by well-marked suture. Mentum broad, with epilobes produced anterad medial tooth. Mentum tooth may be entire or emarginate at the apex, broad or slightly acuminate in form but not sharply pointed. Ligula with glossal sclerite broad at apex, with 2 large apical setae. Paraglossae long and free with cristate microspicules, especially near apex and medially. Labial palpi fusiform, palpomere 2 with 2 large medial setae and 2–3 small apical setae, palpomere 3 with small scattered setae. Maxillae with lacinia large and with thick, curved apical digitus and medial field of large spines. Cardo distinctly developed, stipes with 2 large setae, 1 apical 1 basal. Palpifer simple, maxillary palpi fusiform. Palpomere 1 broad with few small setae at apex, palpomere 3 very short relative to palpomere 4 and with several small setae at its apex, palpomere 4 with scattered small setae, 2 lateral setae larger in most individuals. Galea with 2 small terminal setae. Mandibles with retinaculum discrete, premolar and molar teeth small.

Thorax. Ventral thoracic segments impunctate except for a few punctures on mesepisternum in some individuals, shiny, microsculpture obsolete or faint, irregular mesh, or slightly transverse. Pronotum variously formed, lateral margins sinuate or subsinuate in most species, apical margin straight or front angles slightly produced, basal margin straight or bi-sinuate, inner basal foveae present, sharply impressed in most species, outer basal foveae quite variable among species and somewhat variable among individuals. Prosternal process apically margined. Metepisternum longer than wide. Flight wings full (Fig. 7C) in all individuals investigated. Elytra oblong-ovate, free at suture, broad across humerus and

humeri angulate in most species, slightly wider than pronotum; striae deep, smooth; stria 1 continuous with parascutellar stria; intervals convex to flat; third interval broader than other intervals in some species, notably in species of the *A. aenea*-group; each elytron with a single setigerous dorsal puncture in third interval behind middle, in contact with second stria in most individual. Legs slender and of moderate length. Metacoxal anterior sulcus appressed along anterior margin (Fig. 3B), or divergent, and arcuate/sinuate ended medially in coxa (Fig. 3A), coxae with two setae. Pro- and mesotrochanters with a single large seta, metatrochanter apically rounded or slightly pointed, without setae. Femora slender, setation various between species and individuals but in most individuals as follows: profemora—anterior face, 1 apical, 1 medial; dorsal face, 1 apical, 1 subapical; posterior face, 1 apical, 1 medial and 1 basal, presence of basal seta quite variable; mesofemora—anterior face, 1 apical, 1 basal and 2 medial; dorsal face with row of 8–16 setae, 2–4 setae apical; posterior face, 0–2 setae; metafemora—anterior face, 1 apical,1 medial; dorsal face with row of 3–4 setae; posterior face glabrous. Tibiae slender; protibia with row of 3–4 fine setae on medial face and row of 3–5 stouter setae laterally, 2 clip setae and anterior brush of fine setae ended at enlarged medial seta; meso- and metatibiae with four rows of prominent setae, medial row with very fine, others rows with much stouter seta. Male protarsomeres expanded, 1–3 with articulo-setae ventrally (Stork, 1980). Female protarsomeres 1–4 as well as meso- and metatarsomeres 1–4 in both sexes with two more or less well-defined rows of ventral setae and numerous, scattered setae that are mostly smaller than row setae; fifth tarsomere with two pairs of fine ventral setae, apical nearly twice length of subapical. Tarsal claws pectinate, with 4–6 small denticles on each claw (Fig. 2A).

Abdomen. Sterna in most species shiny, microsculpture in all species obscure medially, more prominent laterally. Transverse sulcus of sterna V–VI present and entire or medially absent, or completely absent. Male genitalia (Fig. 21–23) either simple, median lobe relatively straight, endophallus minutely spinose and scrotiform, or variously modified with median lobe slightly curved and endophallus with fields of large spines and sacculi. Median lobe smooth in most species, strigose in some species of the *A. picipes*-group. Female gonocoxite-1 with 0–4 small ensiform setae near apex, gonocoxite-2 arcuate and laterally excavated, apex round, 1 dorsal and 1 lateral large ensiform seta, 2 nematiform setae in elongate apical furrow (e.g., Fig. 19A). The gut of a single specimen of *A. splendidula* was dissected (Fig. 7B). Crop (crp) pouched ventrally; proventriculus (pv) with 4 compact, fibrous pads; mid-gut (MG) covered by short similarly shaped crypts (ct) and 4 Malpighian tubules (mt) intertwined along its length; hind-gut (HG) with 5 oval rectal pads (rtp). Pygidial gland reservoir (rs) simple, oval (Fig. 7A), efferent duct (eff) broad, subequal in length to reservoir. Collecting canal (cc) short, ramified 10–12 times, each ended with secretory cell (sc). Collecting canal 1 mm long approximately 2× length of efferent duct, efferent duct joined by canal just above midpoint.

Defensive chemical compounds. Methacrylic and tiglic acids, undecane, dodecane and tridecane produced by pygidial glands (Will et al., 2000, 2001).

Species Accounts

Subgenus *Abaris sensu stricto*

Cladistic Diagnosis.—All members of this clade share the synapomorphic laterally sulcate basal bulb of the aedeagal median lobe (Fig. 21B, Fig. 31: character 19).

A. striolata-group

Cladistic Diagnosis.—Individuals of this group have the tip of the aedeagus very thin, blade-like in the lateral view (Fig. 21A–B,D, Fig. 31: character 22) and the appended gland of the spermatheca (sg) elongate (Fig. 19B, Fig. 31: character 30).

(1)*Abaris napoensis*, **new species**
Fig. 11, 18A, 19A–B, 21A–C, 24A

Type Material.—HOLOTYPE. Male, labeled: "Ecuador, Napo: Onkone Gare Camp, 00°39′10″S, 76°26′00″W, 220 m, terra firma forest, flowerfall-leaf litter; at night; 5&8.X.1995; 07-95. T.L. Erwin Ecuador Expedition 1995, G.E. Ball & D. Shpeley", USNM. ALLOTYPE. Female, same data as holotype, USNM. PARATYPES. 2 females, same data as holotype, UASM, CMNH. 7 males, same data as holotype, UASM(4), CMNH(1), QCAZ(1), KWWC(1).

Type Locality.—As given for holotype.

Range.—Ecuador (Fig. 11).

Recognitory Diagnosis.—The prominent baso-lateral punctation of the pronotum (Fig. 24A) and form of the tip of the aedeagal median lobe (Fig. 21A–C) are distinctive. Photograph of dorsal view figure 18A.

Description.—Medium sized, overall length 6.5–6.8 mm. Very shiny, aeneous head and pronotum darker than virescent elytra. Ventral body surface, legs, mouthparts and antennae ferrugino-testaceous; legs and abdominal sterna slightly paler than other areas.

Head. Ocular ratio 1.80–1.84. Head very shiny, reticulate microsculpture scarcely visible, frontal impressions deep, short, slightly convergent, not clearly delimited medially, clypeus shallowly depressed apically and laterally. Mentum tooth form simple, broad.

Thorax. Pronotum (Fig. 24A) sinuate laterally; basolateral region reflexed in basal third of pronotum but slightly convex near hind angles; front angles scarcely produced; apex not narrowly constricted; hind angles denticulate; lateral bead broad in basal third, then sharply narrowed to hind angles; basolateral margin not bordered; microsculpture on disc very faint, transverse mesh. Elytra with transverse microsculpture; basal section of stria 1 present; intervals 2–3 equal width, intervals flat; humeral tooth produced anterad interval 8. Mesepisternal angle produced as small rounded tubercle. Metacoxal sulcus arcuate, ended medially in coxa (in some specimens sulcus very short and so not arcuate, but still divergent from apical margin).

Abdomen. Sterna V–VI with lateral sulci. Basal bulb of male median lobe laterally sulcate (Fig. 21A–C), endophallus folding pattern visible in cleared lobe; blade smooth, sinuate; tip thin, reflexed, with broad asymmetrically expanded area. Female reproductive tract (Fig. 19B) seminal canal broad with few loose twists, receptaculum not discrete from canal, expanded base of seminal canal very large and continuous with bursa, appended gland elongate; gonocoxite-1 with 3 apicolateral ensiform setae.

Etymology.—Specific epithet is Latinized adjective based the type region.

(2)*Abaris striolata* Bates, 1871
Fig. 16, 21D–E, 24B

Abaris striolata Bates, 1871:220.

Type Material.—LECTOTYPE (here designated). Male, labeled: "Ega" [handwritten]; "Abaris striolata type, Bates" [handwritten]; "Ex Musaeo H.W. Bates, 1892", MHNP.

Type Locality.—Brazil, Tefé [Ega]. From original description.

Range.—Brazil, Peru (Fig. 16).

Recognitory Diagnosis.—Individuals small, with the pronotal base smooth in most individuals, outer basal foveae shallow, and baso-lateral region reflexed. Best separated from other species by the characteristic pronotum (Fig. 24B) and character combinations in the key.

Description.—Small sized, overall length 5.3–6.2 mm. Elytra cupreous, head and pronotum black with slight metallic reflection. Ventral body surface, mandibles and labrum piceous; legs, palpi and antennae ferruginous to brunneous.

Head. Ocular ratio 1.71–1.90. Mentum tooth emarginate at apex. Microsculpture of head obsolete; frontal impressions short, deep, parallel.

Thorax. Pronotal basolateral region convex, apex broad, front angles not produced, hind angles denticulate, lateral bead narrow, basolateral margin not bordered (Fig. 24B); microsculpture on disc transverse. Microsculpture of elytra transverse, basal section of stria 1 present, elytral humeral tooth anterad interval 8; intervals flat on disc, more convex laterally, intervals 2–3 of equal width. Metacoxal sulcus arcuate, ended medially in coxa. Mesepisternal angle produced as small sharp tubercle.

Abdomen. Abdominal sulci present laterally on sterna V–VI. Basal bulb of male median lobe laterally sulcate; endophallus folding pattern visible; tip thin in lateral profile, asymmetrical in dorsal/ventral views (Fig. 21D–E). Female tract with seminal canal broad, straight; receptaculum not discrete from canal; spermatheca without basal bulb, expanded base of seminal canal large and continuous with bursa; appended gland elongate; gonocoxite-1 with 2 apicolateral ensiform setae.

Notes on Life History.—Adults have been collected in July and September–

November at elevations of 290–840 m. A single specimen was collected at mercury vapor light and one at a "Fig fall." Other notes include collections in subtropical moist forest, leaf litter in a dry stream or simply "on ground."

Material Examined.—In addition to type, 12 specimens. **PERU. Cusco:** Quincemil [MCZC]. **Junín:** San Beni Valley 8 km E Satipo [SEMC]. **Madre de Dios:** Río Tambopata Reserve, 30 km (air) SW of Puerto Maldonado [USNM]; Río Tambopata Reserve, 30 km (air) SW of Puerto Maldonado 12°50′S, 69°20′W [BMNH, DHK]. Tambopata Reserve, 30 km (Air) SW of Puerto Maldonado, main trail -tf, 12°50′S, 69°20′W [USNM].

A. aenea-group

Cladistic Diagnosis.—All members of this clade have the lateral area in the basal third of the pronotum reflexed and flat laterad the outer basal foveae (Fig. 31: character 13). A similar condition is known in species of *Prosopogmus* and other Carabidae. These other occurrences of this condition are considered analogous.

(3)*Abaris robustula* Tschitschérine, 1898
Fig. 15, 21F–G, 24C

Abarys robustulus Tschitschérine, 1898:83.

Type Material.—HOLOTYPE. Female, labeled: "Mih'om" [questionable interpretation of handwriting], "Abarys robustulus m. typ. Tschitscherin det" [handwritten name on printed determination label], "Coll. Mus. Vindob, TYPUS" [red paper], NMW.

Type Locality.—Brazil, as given in original description.

Range.—Bolivia, Brazil, Peru (Fig. 15).

Recognitory Diagnosis.—Pronotum distinctive with outer basal foveae absent and a nearly flat, reflexed area along the margin (Fig. 24C). Very similar in general facies to *A. striolata* but male median lobe is straighter and thicker at the tip (compare Fig. 21D–E to Fig. 21F–G).

Description.—Small sized, overall length 6.4–6.9 mm. Black with aeneous luster, less pronounced on head and pronotum. Ventral body surface, mandibles and labrum piceous; legs, palpi and antennae paler brunneous.

Head. Ocular ratio 1.62–1.88. Mentum tooth shallowly emarginate at apex. Microsculpture of head faint, nearly effaced on disc, reticulate, micropunctulae present in some individuals (visible at 25×). Frontal impressions short, shallow, not clearly delimited medially.

Thorax. Pronotal (Fig. 24C) basolateral region reflexed, apex broad, front angles produced, hind angles denticulate, lateral bead narrow, margin sinuate to base, basolateral margin not bordered, outer basal foveae absent, inner punctiform; microsculpture on disc transverse, faint and shiny. Microsculpture of elytra transverse; basal section of stria 1 present, intervals 2–3 of equal width, intervals flat to slightly convex; elytral humeral tooth anterad interval 8. Metacoxal sulcus arcuate.

Abdomen. Shallowly sulcate laterally on sterna V–VI. Basal bulb of male median lobe laterally sulcate, median lobe with subapical expansion visible in dorsal view (Fig. 21F–G); endophallus folding pattern visible. Female reproductive tract with seminal canal narrow with many tight twists, receptaculum distinct, spermatheca without basal bulb, appended gland spherical; gonocoxite-1 with 2–3 apicolateral ensiform setae.

Notes on Life History.—Collected in September, October and November at elevations of 400–750 m. The Pakitza specimen was collected in the leaf litter in a dry, stony stream and the Bolivia specimen was taken at mercury vapor light.

Material Examined.—In addition to type, 4 specimens. **BRAZIL.** unknown [NMW].

PERU. Madre de Dios: Pakitza, Zone-3, 12°07′S, 70°58′W; In leaf litter of stony dry stream, Trail Castanal [USMN]. **Cuzco:** Quincmil, Peña.[MCZC].

BOLIVIA. Santa Cruz: Ichilo Province, Buena Vista [CMNH].

(4)*Abaris aenea* Dejean, 1831
Fig. 5, 8, 14, 18C, 21H–I, 24D–E

Abaris aenea Dejean, 1831:781.

Type Material.—LECTOTYPE, (here designated). Male, labeled: "♂" [drawn on green paper]; "aenea. mihi, Carthagena" [handwritten on green paper]; "ex Museo, Chaudoir" [red ink], MHNP.

Abaris darlingtoni Straneo, 1939:38. [**New Synonymy**].

Type Material.—HOLOTYPE. Male, labeled: "Barro Colorado, Canal Zone, May 17 1929, Darlington; 23393, MCZC. Type, darlingtoni" [red paper]; "Holotype" [red paper]; "Abaris darlingtoni, Holotypus n.sp., det. ing. Straneo; ADP, 03439; ♀ winged"; MCZC. ALLOTYPE. Female labeled: "Barro Colorado, V.18.26, C.Z. Van Tyne" [handwritten]; Allotype [red paper], "77" [red], "Darlingtoni Straneo", MSNM.

Type Locality.—Cartagena, Bolivar, Colombia.

Range.—Colombia, Ecuador, Panama, Peru, Venezuela (Fig.14).

Recognitory Diagnosis.—Small and very shiny. Similar to *A. erwini* but distinguished by the obsolete microsculpture of the head and pronotum. Habitus figure 18C.

Description.—Small sized, overall length 5.0–6.0 mm. Bronze or virescent, head and often pronotum darker and greener than elytra. Ventral body surface brunneous, legs and mouthparts paler rufous or ferrugino-testaceous.

Head. Ocular ratio 1.71–1.83. Clypeus medially tumescent, apically and laterally depressed and finely strigate or rugose in region near hind setigerous puncture, frontal impressions parallel. Microsculpture absent except as faint mesh on depressed portion of clypeus; scattered micropunctulae on dorsum. Mentum tooth slightly emarginate at apex.

Thorax. Pronotum (Fig. 24D–E) flat and reflexed in basolateral region, apex broad, front angles slightly produced, margins subsinuate to base and broadly reflexed in basal half; lateral bead of uniform width throughout, irregularly punctulate-rugose in basal quarter. Some specimens with faint rugosities and punctulae along lateral margin (Fig. 24E) (This is constant and more developed in specimens from Ecuador, only slightly punctate in specimens from Peru and mixed in specimens from Panama. In all specimens pronotum is smoother than in *A. notiophiloides*, though approaching the condition in that species in Ecuadorian populations). Hind angles slightly denticulate. Elytral microsculpture transverse; basal section of stria 1 absent, intervals slightly convex, interval 3 width 1.2–1.57× interval 2 (see synonymy below). Metepisternal angle produced as small round tubercle. Metacoxal anterior sulcus arcuate, ended medially in coxa.

Abdomen. Sterna without sulci. Basal bulb of male median lobe laterally sulcate, endophallus structure visible in repose as a darker medial area in cleared lobe (Attempts to evert endophallus only succeeded to expose it half way. From this, it appears to be scrotiform, uniformly covered with spines, without sacculi.) Female tract with seminal canal long and narrow, with numerous tight twists, receptaculum distinct, appended gland spherical; gonocoxite-1 with 1–2 apicolateral ensiform setae.

Chemical data. Defensive chemicals secreted from the pygidial glands are methacrylic and tiglic acids, undecane, dodecane and tridecane (Will et al., 2000, 2001).

Notes on Life History.—Adults have been collected in all months of the year except April and September, most commonly at 150–200 m elevation. Specimens have been collected mostly at night and in thin, relatively dry leaf litter. Several Ecuadorian specimens were collected in primary tropical forest on a well-drained ridge in red clay soil by raking leaf litter and scraping the humus and root layer beneath ferns at night. Although rotten *Ficus* fruits were found nearby—and in association with the fruit a species of *Pseudabarys* Chaudoir and several species of Harpalini—*A. aenea* was not found to be associated with the fruit. Specimens have been collected in leaf litter and at flower falls both during the day and night at several sites. A few specimens have been taken at ultraviolet or white lights.

Synonymy.—Straneo (1939) described *A. darlingtoni* from Barro Colorado Is., Panama. Given the small amount of material at his disposal, Straneo determined

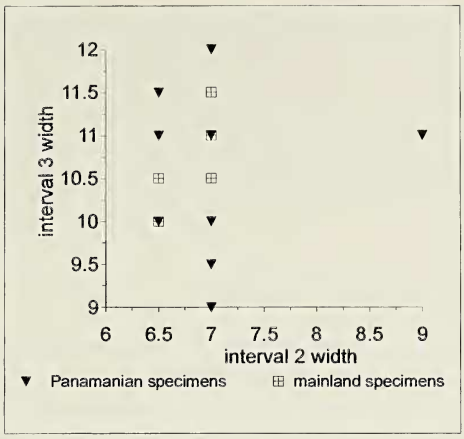

Fig. 8.—Graph of width ratio of elytral intervals for specimens of *Abaris aenea* Dejean. Average ratio of interval 3(Y axis)/2(X axis). Units on axes in ticks of ocular reticle. Standard deviation and number of individuals measured: "darlingtoni" Panamanian form, 1.57 ± 0.04, n = 12; Columbia, 1.45 ± 0.31, n = 6; Venezuela, 1.47 ± 0.27, n = 3; Ecuador, 1.50 ± 0.13, n = 4.

that specimens with a relatively wider third elytral interval, as compared to *A. aenea*, combined with a lack of lateral pronotal punctures, as in *A. notiophiloides*, belonged to a distinct species. Based on the larger amount material I have at hand, it is clear that interval width variation is not a sufficient character for species recognition in this complex.

Individuals were measured for the ratio of interval 3/interval 2 from all collecting sites, representing both South American *A. aenea* and the Panamanian "*darlingtoni*" form (Fig. 8). No discrete difference can been seen when all data are compared. Individuals from the island population are very similar to each other, but are within the variation seen in the Venezuelan, Ecuadorian and Colombian populations. Similarly, all other characteristics show no difference among populations of *A. aenea* that are not subsumed by variation between individuals. Likewise, the Panamanian "*darlingtoni*" form is not distinguishable from South American specimens of *A. aenea*.

Material Examined.—133 specimens. **COLOMBIA:** [IZWP]; Cartagena [BMNH, MHNP]; Río Frío, Magdalena [MCZC].

ECUADOR. Napo: Onkone Gare Camp, 0°39′10″S, 76°26′0″W [UASM]; Limoncocha [UASM]; Yasuni Scientific Station, 00°40′36″S, 76°24′02″W [KWWC, CUIC].

PANAMA. Canal Zone: Barro Colorado Island [CMNH, MCZC], 9°9′15″N, 79°15′0″W, [USNM]; Chepo, Altos de Maje [STOC].

PERU. Madre de Dios: Río Tambopata Reserve, 30 km (air) SW Pto., Maldonado, 12°50′S, 06°20′W [BMNH]; Río, Tambopata Reserve, 30 km, (air) SW of Puerto Maldonado, 12°50′S, 69°20′W [DHK].

VENEZUELA. [MHNP]; San Esteban [MHNP].

(5)*Abaris erwini*, **new species**
Fig. 11, 18B, 21J–M, 24F

Type Material.—HOLOTYPE. Male, labeled: "Peru: MADRE DE DIOS, Pakitza, Zone 02, 9&12 Feb90 T L Erwin, 70°58′W 12°07′S; Under leaves and, fallen fruit, Tr. Aguajal 107; BIOLAT,COLE, 000007170", USNM. ALLOTYPE. Female with same data except last label, "BIOLAT,COLE, 000007153", USNM. PARATYPES. 5 males with the same data as the Holotype except the following labels; BIOLAT,COLE, 000007156; BIOLAT,COLE, 000007152; BIOLAT,COLE, 000007154; BIOL-

AT,COLE, 000007155; BIOLAT,COLE, 000002472, USNM, and 5 females with the same data as the holotype except the following labels; BIOLAT,COLE, 000007157; BIOLAT,COLE, 000007169; BIOLAT,COLE, 000007164; BIOLAT,COLE, 000007156; BIOLAT,COLE, 000007154, USNM. Female, Chambireyacu, pres Yurimaguas, (Huallaga-Pérou), M. de Mathan, Juin–Août 1885, MHNP. Female, Peru, Madre de Dios, Río Tambopata Res., 30 km (air) sw Pto., Maldonado, 12°50′S 069°20W; B.M.1983.455, N.E. Stork, 3.x.–15.xi.1983, on ground, BMNH. Male, Peru: Tambopata Prov., Madre de Dios Dplo.15 km NE Puerto; Maldonado, Reserva, Cuzco Amazónica, 12°33′S, 69°03′W, 200 m, Plot #Z1E9; 17 June 1989, J.S Ashe, R.A.Leschen #136, ex. Flight intercept trap, SEMC. Male, Peru, Junín San Ramón de Pangoa 40 km SE Satipo, Schuh, R.T.& J.C., 7 June 1972, Soils-litter layer in primary forest, AMNH.

Type Locality.—As given for holotype.

Range.—Peru, Bolivia (Fig. 11).

Recognitory Diagnosis.—Small and shiny, somewhat variable species, separated from *A. aenea* by the more evident microsculpture on the head and generally less punctate pronotum. Separated from other similar species by characters in the key. Photograph of dorsal view figure 18B.

Description.—Small sized, overall length 5.3–5.9 mm. Shiny, aeneous, head and pronotum darker, virescent. Ventral body surface, labrum and mandibles dark brunneous; legs either brunneous or sightly paler than venter of body; tibiae, tarsi palpi and distal antennomeres paler.

Head. Ocular Ratio 1.73–1.78. Frontal impressions short, parallel, shallow, sharply delimited externally. Mentum tooth slightly emarginate at apex. Microsculpture of head very faint, reticulate.

Thorax. Pronotal basolateral region slightly convex though obscured in some individuals by punctures; apex broad, front angles little produced, margins subsinuate; hind angles not denticulate, lateral bead uniform thickness throughout or narrowed in apical quarter, basolateral margin not bordered; microsculpture transverse, very faint, shiny. Elytral microsculpture transverse; basal section of stria 1 absent, intervals flat, interval 3 width 1.1–1.4× interval 2, mesepisternal angle produced as low flat tubercle; elytral humeral tooth anterad interval 8. Metacoxal sulcus arcuate, ended medially in coxa.

Abdomen. Sterna without sulci. Male aedeagus (Fig. 21J–M) with basal bulb of median lobe laterally sulcate (Fig. 21J, bs); endophallus folding pattern visible in cleared lobe (I attempted to evert the endophallus of several specimens but the internal sac only everted half way. A basal right sacculus covered in medium length spines was apparent on everted portion); median lobe blade smooth. Female tract with seminal canal thin with many tight twists, receptaculum distinct, appended gland spherical; gonocoxite-1 with 3 apicolateral ensiform setae.

Variation.—In regard to pronotal form, this species is rather variable and may prove to be a complex of species rather than one polymorphic species.

Notes on Life History.—Adults have been collected in January, February, June, July and September–November at elevations of 200–750 m. Specimens were collected in leaf litter and in areas with fallen rotten fruits, such as *Ficus* fruits.

Material Examined.—29 specimens examined, including types. **BOLIVIA.** Chapare [MSNM].

PERU. Huallaga: Yurimaguas, Chamireyacu [MHNP]. **Junín:** San Ramón de Pangoa 40 km SE Satipo [AMNH]. **Madre de Dios:** Pakitza, 12°7′0″S, 70°0′0″W [USNM]; Pakitza, Río Manu, BIOLAT Sta. 11°56′47″S, 71°17′0″W [USNM]; Pakitza, Zone 04, 12°7′0″S, 70°0′0″W [USNM]; Río Tambopata Reserve, 30 km (air) SW of Puerto Maldonado, 12°50′0″S, 69°20′0″W [CASC]; Río Tambopata Reserve, Explorer's Inn 12°50′0″S, 69°17′0″W [USNM].

Etymology.—Eponym based on the surname of the collector and carabidologist Terry L. Erwin.

(6)*Abaris aquilonaria*, **new species**
Fig. 12A, 20A, 21N–O, 24G

Type Material.—HOLOTYPE. Female, labeled: "Mexico, Chiapas, 3200′. 11.6 mi. N Ocozocuautla, vi.10–13.1966; George E. Ball, D.R.Whitehead collectors", USNM. ALLOTYPE. Male, labeled: "Coyame, Lake Catemaco, Veracruz, Mexico, 10–18.VII.63-Black lts. D.R.Whitehead", USNM. PARATYPES. Female, label data same as holotype, UASM. Female, labeled: "Mexico, Chiapas 11.6 mi.N Ocozocoautla, 3200′, May 25 & June 20 '72, A.Meyer, G.E.& K.E. Ball, Collectors", UASM. Male, same label data as allotype, KWWC. Male, genitalia dissected, labeled: "Mexico, Chiapas,

Parque Laguna Belgica 19 km N.Ocozocoautla, 2 June 1991, 970 m, J.S.Ashe Coll#46, ex; flight intercept trap", SEMC.

Type Locality.—As given for holotype.

Range.—Costa Rica, Honduras, Mexico (Fig. 12A).

Recognitory Diagnosis.—Similar to *A. aenea* but the presence of visible microsculpture on the pronotum and the lack of punctation along the base immediately distinguishes *A. aquilonaria.*

Description.—Small sized, overall length 5.4–6.1 mm. Shiny, aeneous, with head and pronotum slightly darker. Ventral body surface dark brunneous; legs, antennae and mouthparts paler brunneous to ferrugino-testaceous.

Head. Ocular ratio 1.74–1.85. Mentum tooth slightly emarginate at apex, microsculpture of head faint, reticulate. Frontal impressions short, deep, not clearly delimited medially. Clypeus smooth or with a few shallow lines.

Thorax. Pronotum (Fig. 24G) with obvious, slightly transverse mesh microsculpture; region laterad of basal foveae flat and reflexed, apex broad, front angles not produced, hind angles denticulate, lateral beads uniform or slightly narrower at hind angles, lateral margins sinuate to base. Metacoxal sulcus arcuate, ended medially in coxa. Basal section of elytral stria 1 absent; intervals slightly convex. Elytra with interval 3 width 1.5–2.1× interval 2, humeral tooth anterad interval 8; microsculpture transverse.

Abdomen. Sterna without sulci. Basal bulb of male median lobe laterally sulcate, blade smooth (Fig. 21N). Female reproductive tract (Fig. 20A) with seminal canal long, narrow with a few (4–5) tight twists, receptaculum distinct, appended gland (sg) spherical; gonocoxite-1 with 2 apicolateral ensiform setae.

Notes on Life History.—Adults collected in May–July at elevations of 700–970 m. Collections have been made using flight intercept traps and ultraviolet lights.

Material Examined.—6 specimens in addition to types. **COSTA RICA. Guanacaste:** Guanacaste Conservation Area, Martínez Biological Station [CASC]. This specimen was not included in the type series as it differs in color (bright green) and the pronotum has longer straight sections in front of the hind angles. However, no other differences could be found in the external characteristics or the median lobe of the aedeagus. Additional material of *A. aquilonaria* will either show population level variation that includes this form, or the necessity of describing a new species.

HONDURAS. San Juan Pueblo [USNM]. This specimen is all black, much duller, and the pronotum is somewhat flatter without the sharp denticles of the hind angles of the pronotum found in the typical *A. aquilonaria.* Unfortunately, genitalia of this male specimen are lost. In general form it is quite similar to typical specimens but, like the Costa Rican form, may represent another species. Again, additional material is needed. [USNM].

MEXICO. Chiapas: 11.6 mi.N Ocozocoautla. **Veracruz:** Coyame, Lake Catemaco [UASM, teneral and damaged specimens not included in type series]

Etymology.—Latin adjective *aquilonaris* (northern). This refers to the fact that this species ranges farther north than any other *A. aenea*-group species.

(7)*Abaris notiophiloides* Bates, 1871
Fig. 11, 19C, 21P–Q, 24H

Abaris notiophiloides Bates, 1871:220. Abarys notiophiloides (Chaudoir, 1873:98).

Type Material.—LECTOTYPE (here designated). Female: Labeled: "Ega" [Handwritten]; "Ex. Museao H.W.Bates, 1882", "Abaris notiophiloides Bates type" [Handwritten]; "Lectotype Abaris notiophiloides Bates, K.W.Will 1997" [red paper label], MHNP.

Type Locality.—Brazil, Tefé [Ega], from original description.

Range.—Brazil (Fig. 11).

Recognitory Diagnosis.—Immediately recognizable by the greatly widened elytral interval 3 in combination with the punctate pronotal margins.

Description.—Small sized, overall length 4.8–5.1 mm. Brunneous with a cupreous luster, head and

pronotum in most individuals, some with only head, slightly darker. Ventral body surface somewhat paler; legs, palpi and antennae paler.

Head. Ocular ratio 1.79–1.86. Mentum tooth shallowly emarginate at apex. Microsculpture of head reticulate, frontal impressions short, divergent, not clearly delimited medially.

Thorax. Pronotal (Fig. 24H) basolateral region flat and reflexed, apex broad, front angles not produced, punctate along margin anterior to outer foveae; margins sinuate, hind angles denticulate, lateral bead narrow and of uniform thickness, basolateral margin not bordered; microsculpture transverse on disc, more irregular at base and near foveae. Elytra with basal section of stria 1 absent, intervals moderately convex, flatter dorsally, interval 3 width 2× width of interval 2, elytral humeral tooth anterad interval 8; microsculpture transverse, faint. Mesepisternal angle produced as small flat tubercle. Metacoxal sulcus arcuate, ended medially in coxa.

Abdomen. Sterna without sulci. Basal bulb of male median lobe laterally sulcate, endophallus folding pattern visible, blade smooth (Fig. 21 P–Q). Female reproductive tract (Fig. 19C) with seminal canal short, broad, straight, receptaculum not discrete from seminal canal, without basal bulb, fibrous region at base of spermatheca, appended gland spherical, gonocoxite-1 with 2 apicolateral ensiform setae.

Notes on Life History.—Found together with *Pseudabarys robustus* (Bates) (Bates, 1871:220).

Material Examined.—Including types, 12 specimens examined. **BRAZIL.** Chapada [MSNM]; Ega [MHNP]; Itaituba, Amazones (Hahnel) [MHNP]; Santarém [CMNH]; Unknown; [MHNP].

A. picipes-group

Cladistic Diagnosis.—Members of this clade have either faint or obsolete transverse microsculpture on the pronotal disc and the region near the basal foveae (Fig. 31: characters 16, 17). This clade includes some of the most widespread and variable species in the genus. Although the general form and internal structures of the male genitalia are similar among all species in the clade, it is not possible to define any non-homoplasious synapomorphies of the male genitalia that characterize the clade at the level of the species-group. Within the group, strigose ventral surface of the median lobe (character 21) found in *A. mina, A. picipes*, and *A. basistriata* is a synapomorphy for those species. The median lobe of *A. metallica* is not known, but is predicted to be strigose as well (Fig. 31).

(8)*Abaris impunctata*, **new species**
Fig. 15, 21R–S, 24I

Type Material.—HOLOTYPE. Male, labeled: "Brazil, Santa Catarina, Nova Teutonia, 27°11′0″S, 52°23′0″W, 300–500 m, F.Plaumann", MCZC.

Type Locality.—As given for holotype.

Range.—Brazil (Fig. 15).

Recognitory Diagnosis.—Recognizable, dark species with dull surface from reticulate and somewhat granulate microsculpture and impunctate pronotal base (Fig. 24I).

Description.—Medium sized, overall length 7.0 mm. Black with a slight aeneous luster. Ventral body surface, legs and mouthparts brunneo-piceous.

Head. Ocular ratio 1.67. Mentum tooth form simple. Microsculpture of head reticulate; frontal impressions short, punctiform.

Thorax. Pronotal basolateral region convex, apex broad, front angles very slightly produced, hind angles minutely denticulate; lateral bead of uniform width through most of its length narrowed just before hind angles; basolateral margin not bordered (Fig. 24I); microsculpture reticulate and surface dull. Microsculpture of elytra obvious, reticulate; basal section of stria 1 present, intervals flat, intervals 2–3 equal width, mesepisternal angle produced as small flat tubercle; humeral tooth anterad interval 8. Metacoxal sulcus arcuate, ended medially in coxa.

Abdomen. Sterna V–VI shallowly sulcate laterally, deeper on VI where it is oblique to base of

sternum. Male median lobe (Fig. 21R–S) basal bulb laterally sulcate, endophallus folding pattern visible in cleared median lobe, blade smooth, tip symmetrical. Female genitalia and reproductive tract not studied.

Etymology.—Specific epithet is a Latin adjective referring to the lack of obvious punctures along the base of the pronotum.

(9)*Abaris bigenera* Bates, 1882
Fig. 12B, 19D, 22A–D, 25A

Abaris bigenera Bates, 1882:86. Larval description by Bousquet and Liebherr (1994).

Type Material.—LECTOTYPE, (here designated). Male, labeled: "Oaxaca, Mexico. Hoege", BMNH.

Type Locality.—Mexico, Oaxaca, from original description.

Range.—Guatemala, Honduras, Mexico (Fig. 12B).

Recognitory Diagnosis.—One of the most common Mexican species. Easily separated from the other common Mexican species, *A. aequinoctialis*, by the larger size and more somber color. Relatively large and dark species, frontal impressions effaced, rather variable but recognizable using characters in the key.

Description.—Variable in size but most relatively large sized, overall length 6.4–7.9 mm. Dark, moderately shiny, metallic luster faint, cupreous in most individuals, but striking blue or green in a few individuals; head and pronotum concolorous with elytra in most, darker in some individuals. Ventral body surface brunneous; legs, mouthparts and antennae slightly paler but infuscated in some individuals, especially mandibles, antennae and femora.

Head. Ocular ratio 1.68–1.80. Mentum tooth shallowly emarginate at apex. Microsculpture of head reticulate; frontal impressions short, shallow and convergent or effaced.

Thorax. Pronotal margins smoothly arcuate or subsinuate to hind angles that are either minutely denticulate or not; apex wide, front angles slightly produced, lateral bead narrow and uniform throughout its length, basal margin not bordered, basolateral region slightly convex; microsculpture reticulate, surface dull. Basal section of elytral stria 1 present, intervals flat, intervals 2–3 of equal width, elytral humeral tooth anterad interval 8; microsculpture transverse; surface moderately shiny. Metacoxal sulcus arcuate, ended medially in coxa. Mesepisternal angle very small, produced as low round tubercle.

Abdomen. Abdominal sulci present laterally on sterna V–VI. Median lobe basal bulb laterally sulcate, endophallus (Fig. 22C–D) with ventral field (vs) of large spines and left and right basal-lateral sacculi (lls, rls), right sacculus recurved, partially spine covered with its position corresponding to spined ridge in *A. basistriata*; median lobe (Fig. 22A) ventrally smooth, lobe tip asymmetrically produced to right (Fig. 22B). Female reproductive tract (Fig. 19D) with seminal canal narrow with many tight twists, receptaculum distinct, appended gland (sg) spherical, gonocoxite-1 with 2, 3 or 4 apicolateral ensiform setae.

Notes on Life History.—Adult specimens have been collected in April–September at elevations of 200–1680 m. When habitat was noted, most specimens were collected in the leaf litter of relatively dry oak-pine forest, e.g., "oak-pine zone, *Alnus* near stream in litter." Specimens were also collected in oak forest, wet oak-pine forest and montane tropical forest. Other habitat associations include coffee finca, crustose fungi and crustose fungi on logs or under logs and gilled mushrooms. In addition to collecting from leaf litter, pan traps were reported as a collection method for some specimens.

Material Examined.—Including type, 223 specimens. **GUATEMALA.** Baja Verapaz, 7.6 km W Chilascó [SEMC]; Baja Verapaz, 1.6 km S Pantin 15°16′0″N, 90°14′0″W [USNM]; Baja Verapaz, 8 km S Purulhá [UASM]; El Quiché, 7.3 m S Chichicastenango 14°54′0″N, 91°7′0″W [USNM]; S Geronimo [MHNP]; Sacatepequez Florencia [UVGC]; El Progreso 21 km NE San Augustíne Acasaguastlán [UASM]; Zacapa Dept., San Lorenzo [CNC]; Sierra de las Minas [CNC].

HONDURAS. Los Piños, 14°32′0″N, 87°53′0″W [UASM]; Ocotepeque 12.7 km E & 10.6 km S Ocotepeque lower slopes El Pital, 14°25′0″N, 89°4′0″W [SEMC]. **Morazán:** Francisco 21.3 km N Teguicigalpa, la Tigra, 12°14′0″N, 86°6′0″W [SEMC].

MEXICO. Chiapas: 6 km SE Tolimen [UASM]; 18.7 km W Rizo de Oro, Chiapas/Oaxaca border [UASM]; 3.1 mi. N Pueblo Nuevo [UASM];3.1 mi. N Pueblo Nuevo, Rte195 [UASM]; 8.6 mi. E San Cristobal, rte 190 [UASM]; El Rincón [CNC]; Lagos de Monte Bello National Park [UASM]; Município de Ocosingo 2nd ridge NE of Las Margaritas above La Soledad [CASC]. **Guerrero:** 12.1 mi. W Chilpancingo [UASM]; 13.9 mi. W Chilpancingo [UASM]; 143.1 km NE Atoyac de Alvarez [UASM]; 2 km SW Yerba Santa 39 km S Filo de Caballo [CMNH]; 52.9 km NE Atoyac de Alvarez [UASM]; 78.5 km N junction Rt200 on rt134 to Ciudad Altamirano [UASM]; B. Vista de Cuellar, "El Pochote" [UASM]; Omiltemi [MHNP, UASM]. **Jalisco:** 10.8 mi. S Talpa de Allende [UASM]; 12.4 mi. S Tecalitan [UASM]; 21.4 mi. S Tecalitan [UASM]; 42.4 km NW Cuatla [UASM]; 5.5 mi. NW Cuatla [UASM]; 7 km S Tequila rd to Microondas [UASM]; 8.8 km NW Cuatla [UASM]; 9.6 km S Tequila on rd to Microondas [UASM]; El Ricon 30.5 mi. NW Los Volcanes [UASM]; Mexico, 2.7 km NE Temazcaltepec, rte130 [UASM]. **Michoacan:** 97.7 km W Apatzingán on road to Dos Aguas [UASM]. **Oaxaca:** 11.4 mi. E Sta. Catarina Juquila [CNC, UASM]; 12.8 mi. E Sta. Catarina Juquila [UASM]; 14.3 km E Ixtlán de Juárez [UASM]; 14.9 km N Sola de Vega [UASM]; 14 km E Mitla (road to Zacatepec) [CUIC]; 15.7 km E Rte190 road to Ojo de Agua [UASM]; 20 mi. S Juchatengo, rt131 [UASM]; 2 km W Capulalpam [UASM]; 4.9 mi. E Sta. Catarina Juquila [UASM], 6.6 mi. E Sta. Catarina Juquila [UASM], 7.3 mi. E Sta. Catarina Juquila [UASM], 11.4 mi. E Sta. Catarina Juquila [UASM], 12.8 mi. E Sta. Catarina Juquila [UASM]; Hoege [MHNP]; NW Sta. María Nizavaguiti 16°41′0″N, 95°50′0″W [UASM]; Hwy135, 23.6 km N Jct190 at Huitzo [CUIC]; Hwy175, 18.3 km S Guelatao (7.5 km N El Punto) [CNC, CUIC]; Rte131, 21.8 mi. N Juchatengo [UASM]; Queretaro, 17.8 mi. E Landa de Matamoros [UASM]; 6.4 mi. E Pinal de Amoles [UASM]. **San Luis Potosí:** 24.7 mi. S Landa de Matamoros [UASM]; 4.3–17.9 mi. E Ciudad del Maíz rte80 [UASM]. **Sinaloa:** 60.9 km E Concordia rte 40. **Veracruz:** 16.4 km S Orizaba on road to Tlaquilpan [UASM]; 2.3 km S Jalapa on rd to Coatepec [UASM].

(10)*Abaris picipes* Bates, 1871
Fig. 13, 18D, 19E, 23A–C, 25B

Abaris picipes Bates, 1871:220.

Type Material.—LECTOTYPE (here designated). Female, labeled: "Tapajos" [handwritten]; "Abaris picipes type, Bates" [handwritten]; "Ex Musaeo H.W. Bates, 1892" [printed], MHNP.

Type Locality.—Brazil, Tapajos, from original description.

Range.—Argentina, Bolivia, Brazil, Paraguay (Fig. 13).

Recognitory Diagnosis.—Very similar in general form to *A. mina* (see description of that species) but can be separated from that species by the punctate pronotal base. Photograph of dorsum figure 18D.

Description.—Small to medium sized, overall length 5.5–6.4 mm. Shiny, black with cupreous luster; less metallic on head and pronotum, head and pronotum slightly darker in most individuals. Ventral body surface brunneous to piceous; legs, mouthparts and antennae concolorous or slightly paler than ventral body surface.

Head. Ocular ratio 1.67–1.74. Mentum tooth shallowly emarginate at apex. Microsculpture of head obsolete, dorsal micropunctulae present; frontal impressions very short, shallow almost effaced.

Thorax. Pronotal (Fig. 25B) basolateral region convex, punctate in region of basal foveae (single female from Bolivia lacks punctures), apex broad, front angles produced, hind angles with or without a small denticle, lateral bead narrow and of uniform thickness, basolateral margin in some specimens with a fine engraved line in form of border at margin beneath lateral foveae; microsculpture of pronotum obsolete; very shiny. Microsculpture of elytra transverse, faint; basal section of stria 1 present, intervals flat, intervals 2–3 of equal width, humeral tooth anterad interval 8. Mesepisternal angle produced as small tubercle. Metacoxal sulcus arcuate.

Abdomen. Abdominal sulci absent in most individulas, but in some present laterally as faintly impressed, irregular lines. Median lobe (Fig. 23A–C), aedeagal basal bulb laterally sulcate, endophallus folding pattern (fp) visible as a large dark region in cleared lobe, spine patch visible in bend of median lobe; blade strigate (Fig. 23A), tip (Fig. 23B) asymmetrically produced to right. Female reproductive tract (Fig. 19E) with seminal canal broad, simple; receptaculum distinct, slightly enlarged relative to canal; appended gland (sg) spherical; gonocoxite-1 with 0–2 apicolateral ensiform setae.

Notes on Life History.—Adults have been collected in January, February, June,

October–December at elevations of 450–1000 m. Habitat associations include forested areas, in leaf litter and in a litter filled ravine.

Material Examined.—In addition to type, 65 specimens. **ARGENTINA.** Mendoza [MSNM]; Tartagal Salta, Dio San Martín [MSNM]; Tucumán [MHNP]; Jujuy Calilegua National Park, Aguas Negras [CNC]; Jujuy Calilegua National Park, Estaca El Cero [CMNC].

BOLIVIA. Santa Cruz: Alto de Chaves Ascencíon [MHNP]; Andrés Ibanez Potrerillo de Guenda, Terebinto 17°40′20″S, 63°27′0″W [CMNH]; Prov. Andrés Ibanez, Vallecito [CMNH]; Sará [CMNH, MSNM]; Villa Montes [UASM].

BRAZIL. Chapada [CMNH,MSNM]; Mtt. Grosso, Corumbá [MCZC]; Santarém [CMNH]; Tapajos [MHNP]; Bahia Bon "jiue-garbe" [illegible handwriting] [MHNP]; Bahia, Encruzilhada [MHNP]; Distrito Federal, 20 km E Brasilia [CNC], Goias, Cuyaba [MHNP]; Río Verde [MHNP]; Jatahy [MHNP]; Minas Gerais, Aquas Vermelhas [CMNH]; São Paulo, Teodoro Sampaio [CMNH].

PARAGUAY. [MNHB]; Dralze [MCZC]; Puerto Bertoni [MCZC]; Sa. Trinidad [MNHB]; Villarrica [MSNM,MCZC]; vic. Horqueta [MSNM, MCZC]; Boquerón Medina-cue [MCZC]; Paraguari, Parc. Nac. Ybycuí [USNM].

UNKNOWN: Molinasque [MCZC]; Salta Urundel [MHNP].

(11)*Abaris mina*, **new species**
Fig. 16, 23D–F, 25C

Type Material.—HOLOTYPE. Female, labeled: "Brazil, Chapada, Acc. No 2966", CMNH. ALLOTYPE. Male, same label data as holotype, CMNH. PARATYPES. Female, same data as holotype and "Oct", CMNH, Female, same data as holotype and "Aug", CMNH. Male, same data as holotype and "Sept", USNM. Male, labeled: "Brazil, Goyaz, Jatahy, Museum Paris, Ex. Coll. M. Maindron, Coll. G. Babault 1930", MHNP. Male, labeled: "Goyaz, Río Verde, Museum Paris, Ex. Coll. M. Maindron, Coll. G. Babault 1930", MHNP. 2 Females, labeled: "Brésil, Jatahy, Prov. De Goyaz, Donchier march 1903, Museum Paris, Ex. Coll. M. Maindron, Coll. G. Babault 1930", MHNP. Female, labeled: "Brazil, 20 km E. Brasilia, DF, III-4-1970,1000 m, JM& BA Campbell", CNC. Female, labeled: "Paraguay, Stapua Cantera" [handwritten], MNHP. Female, labeled: "Paraguay", MSNM. Female, labeled: "vic. Horqueta, Paraguay", MCZC. Female, labeled: "Villarrica, Paraguay, VI-1932, Zool. Mus. Berlin", MNHB. Female, labeled: "Paraguay, leg. Piebrig, Zool. Mus. Berlin", MNHB. Female, labeled: "Bolivia, Santa Cruz, Ichilo Province, Buena Vista, 400 m, R.Ward, mercury vapor light", CMNH.

Type Locality.—Brazil, Chapada.

Range.—Brazil, Bolivia, Paraguay (Fig. 16).

Recognitory Diagnosis.—Very similar in form to *A. picipes* but distinguished from that species by the smooth pronotal base.

Description.—Medium sized, overall length 6.0–6.7 mm. Shiny, black, aeneous, or virescent in some individuals. Ventral body surface, legs, mouthparts and antennae brunneous.

Head. Ocular ratio 1.67–1.74. Mentum tooth shallowly emarginate at apex. Microsculpture of head obsolete, surface shiny; frontal impressions shallow or effaced.

Thorax. Pronotal (Fig. 25C) basolateral region convex, apex broad, front angles produced, lateral margins arcuate almost to hind angles or slightly anterad base; hind angles with or without small denticle, lateral bead narrow, of uniform thickness throughout; basolateral margin without border in most, few specimens with finely engraved line in form of border along base posterad foveae; microsculpture obsolete on disc, very shiny. Microsculpture of elytra transverse; basal section of stria 1 present, elytral humeral tooth anterad interval 8. Mesepisternal angle produced as a very small round tubercle. Metacoxal sulcus arcuate.

Abdomen. Abdominal sulci present as very shallow irregular lateral lines on sterna V–VI, best developed on V. Median lobe (Fig. 23D–F) basal bulb laterally sulcate, endophallus folding (fp) pattern visible as large dark area in cleared median lobe, blade (Fig. 23D) strigate ventrally, tip (Fig. 23E) symmetrically produced. Female tract with seminal canal narrow with many tight twists, receptaculum distinct, appended gland spherical; gonocoxites-1 with 2–3 apicolateral ensiform setae.

Notes on Life History.—Adults have been collected in March, June, and August–November. Only one specimen was labeled with elevation data, a collection at 1000 m.

Material Examined.—Including types, 22 specimens. **ARGENTINA.** Unknown [MCZC].
BRAZIL. Goias, Jatahy [MHNP].
UNKNOWN: [MNHB].
Etymology.—Specific epithet is a Latin adjective that refers to the smoothness of the pronotum of this species.

(12)*Abaris basistriata* Chaudoir, 1873
Fig. 14, 18E, 22E–I, 25D

Abarys basistriatus Chaudoir, 1873:98.

Type Material.—LECTOTYPE, (here designated). Female, labeled: "ex Museo, Chaudoir" [red ink], "Brézil, Schlb-jun" [? Handwritten, not legible], "Lectotype, *Abarys basistriatus* Chd., K.W.Will 1997" [Red label], MHNP.

Type Locality.—Nova Friburgo, Brazil, from original description.
Range.—Argentina, Bolivia, Brazil, Colombia, Paraguay, Peru, Venezuela (Fig. 14).
Recognitory Diagnosis.—Similar to *A. mina* and *A. picipes* in general form but recognizable by the reticulate microsculpture on the dorsum. Photograph of dorsum figure 18E.

Description.—Medium to small sized, overall length 5.4–6.6 mm. Black with aeneous luster, only moderately shiny. Ventral body surface, legs, mouthparts and antennae brunneous.

Head. Ocular ratio 1.74–1.86. Mentum tooth emarginate at apex. Microsculpture of head reticulate; frontal impressions shallow, not clearly delimited medially.

Thorax. Pronotal (Fig. 25D) basolateral region slightly convex, apex broad, front angles produced, hind angles not denticulate; basolateral bead narrow, uniform thickness; basolateral margin not bordered, margins subsinuate or straight to base; microsculpture reticulate, surface dull. Basal section of elytral stria 1 present, (a single specimen from Río Salado, Argentina lacks the basal section of stria 1, except for a slight trace on the right elytron); mesepisternal angles produced as small sharp tubercles, elytral humeral tooth anterad interval 8; microsculpture reticulate, intervals flat, intervals 2–3 of equal width, striae fine. Metacoxal sulcus arcuate ended medially in coxa.

Abdomen. Sterna without sulci. Basal bulb of male median lobe laterally sulcate, endophallus (Fig. 22H–I) with apico-ventral field (als) of large spines extended dorsally near base, prominent ventromedial spined row (sr), a long right lateral scale (ls) that is apically free, and a short dorso-basal scale (dbs) that is spine tipped and held appressed to tip of median lobe when endophallus is everted, median lobe ventrally strigate (Fig. 22E), lobe tip asymmetrical, produced to right. Female reproductive tract with seminal canal long, thin and with many tight twists, receptaculum distinct, appended gland spherical; gonocoxite-1 with 2–3 apicolateral ensiform setae.

Notes on Life History.—Adults have been collected in all months of the year at elevations of 100–3600 m. The two specimens from Huánuco, Peru, labeled 2500–3600 m are from a much higher elevation than known for any other *Abaris* species. It is likely that these represent a chance collection or are mislabeled specimens, as all other records for *A. basistriata* are for elevations of 1550 m or less. The only additional information is from a specimen collected using a flight intercept trap in subtropical humid forest, one marked as collected "under stones" and ten specimens collected at Mercury vapor or ultraviolet lights.

Material Examined.—In addition to type 166 specimens examined. **ARGENTINA.** Eldorado Misiones [AMNH]; Gargas [MHNP]; LaPampa (Pico) [MCZC]; Río Salado [MSNM, MHNP]; Catamarca, S of La Viña, 28°3′0″S, 65°35′0″W [AMNH]; Salta, La Caldera, El Ucuma, 1550 m [CMNC]; San Martín, Tatagal Salt. [MSNM].
BOLIVIA. Santa Cruz: Alto de Chaves Ascencíon [MSNM]; Ichilo, Bueno Vista [CMNH]; Andrés Ibanez Potrerillo de Guenda, Terebinto, 17°40′20″S, 63°27′0W [CMNH]; Sará [CMNH, MNHB].
BRAZIL. [IZWP, MCZC]; Chapada [CMNH]; Guapi [USNM]; Sâo Paulo Curityba [MNHB]; Santarém [AMNH, CMNH]; Bahia, Encruzilhada [MHNP]; Distrito Federal, Estacao Florestal Cabeca do

Veado [CNC]; Goias, Cuyaba [MHNP]; Río Verde [MHNP]; Jatahy [MHNP, MNHB]; Mato Grosso do Sul, R. Caraguata [MCZC]; Minas Gerais Aquas Vermelhas [MSNM]; Belo Horizonte [MHNP]; Lambary [USNM]; Parana, Bocaiuvu [UASM]; Caviuna [AMNH]; nr. Pato Branco [UASM]; Río Grande do Sul, S.Rosa [MCZC]; Sta. Catarina, Nova Teutonia, [CASC, MCZC, USNM]; Nova Teutonia 27°11′0″S, 52°23′0″W [MSNM, MCZC, MHNP, UASM, USNM]; Nova Teutonia, Sa Catharina [MCZC]; nr Chapaco [UASM]; São Paulo, Campos do Jordao [CMNH].

COLOMBIA. NW Sierra N de Sta. María [MCZC].

PARAGUAY. 40 km E Villarrica [MSNM]; vic. Horqueta [MCZC]; Amabay Cerro Cora [USNM]; Central San Lorenzo [MHNM, CMNH].

PERU. Chanchamayo [MSNM]; Río Pampas (Hyw 7) [CASC]; Huanuco [MCZC]; Piedras Grandes [SEMC].

VENEZUELA. [MHNP]; Caracas [MHNP, MNHB]; Aragua, El Limon [MIZA]; Bolivar, Guri Río Caroni [MIZA].

UNKNOWN: [MHNP], [?]Araras-Sp. [USNM]; [?]Delbrando Leme-Sp.[USNM]; [?]Lagoa santa [IZWP]; [?]Río Jan. [MHNP]; [?]Tlupinangu [MHNP].

(13)*Abaris metallica*, **new species**
Fig. 13, 25E

Type Material.—HOLOTYPE. Female, labeled: "Venezuela, Bolivar, Kavanayen, Aug 8 1970; R.E.Dietz IV, 1000 m.", USNM. ALLOTYPE. Male, labeled: "Caracas" [handwritten on green paper other writing is not legible], MNHB.

Type Locality.—As given for holotype.

Range.—Venezuela (Fig. 13).

Recognitory Diagnosis.—Distinctly amariform and so set apart from all other *Abaris* species. Shiny virescent green with a proportionally large head and pronotum that is broadest at the base.

Description.—Medium sized, overall length 5.8–6.3 mm. brilliant green luster. Ventral body surface, mouthparts, antennae and legs ferruginous to ferrugino-testaceous.

Head. Relatively large, ocular ratio 1.71–1.72. Mentum tooth emarginate at apex. Microsculpture of head reticulate; frontal impressions shallow and broad, clypeus anterior margin slightly emarginate.

Thorax. Pronotal (Fig. 25E) front angles produced, hind angles obtuse, not denticulate, lateral bead very narrow and uniform throughout, basolateral margin not bordered although obscure impression along margin suggests border; microsculpture distinct, reticulate, shiny. Elytra broad, humeral angles prominent, microsculpture on disc reticulate and surface shiny, basal section of stria 1 present, intervals flat dorsally, 2–4 very wide; striae 3–5 almost effaced dorsally; elytral humeral tooth anterad interval 8. Mesepisternal angle produced as prominent, sharp tubercle. Metacoxal sulcus arcuate, ended medially in coxa.

Abdomen. Abdominal sulci complete, finely engraved, very shallow medially. Male genitalia and female genitalia and reproductive tract not studied.

Etymology.—Specific epithet is a Latinized adjective referring to the metallic luster of this species.

Subgenus *Abaridius* Chaudoir, 1873:97

Type Species.—Abaris tachypoides Bates.

Cladistic Diagnosis.—Support for this clade comes from two homoplasious characters; form of the pronotal bead (character 15) and the microsculpture in and near the lateral foveae (character 17). A wide bead that sharply narrows before the hind angles is characteristic of the basal grade species and a more uniform bead is characteristic of species in the clade including *A. tachypoides* and the remaining species (Fig. 32: character 15). The wider/narrowing lateral bead is also known from *A. napoensis* but is hypothesized as a convergent occurrence. The second character, microsculpture in and near the lateral foveae, is highly homoplasious in regard to the selected phylogenetic hypothesis for the genus. The basal species of *Abaridius* have a generally shiny surface, and very faint and

Fig. 9.—Dorsal habitus, *Abaris tachypoides* Bates.

transverse microsculpture in this region, whereas most derived members have reticulate and more or less obvious microsculpture.

Two species, *A. bicolor* and *A. nobilis*, included in the subgenus *Abaridius* lack the more convincing synapomorphies of the *A. tachypoides*-group (see below) and are considered *sedis mutabilis* within the subgenus. Both are large and brilliantly metallic, but otherwise not particularly similar to each other. The form of the pronotum is quite different between the two, with *A. bicolor* (Fig. 25F) more similar to *A. inflata* (Fig. 26B) or *A. nitida* (Fig. 25H), whereas *A. nobilis* has a pronotum that is unique in the genus. Neither male nor female genitalia have been studied for either species as each is represented by only a single

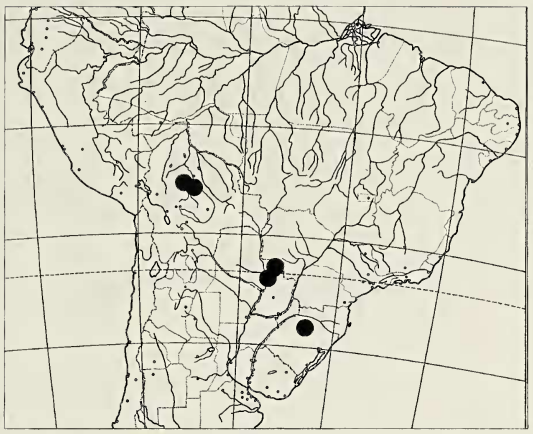

Fig. 10.—Locations of collecting sites for *Neotalus portai* (Straneo) specimens in South America.

specimen. Characteristics of these systems may resolve the relationships of these taxa.

(14)*Abaris bicolor*, **new species**
Fig. 15, 25F

Type Material.—HOLOTYPE. Male, labeled: "Ecuador, Napo, Onkone Gare Camp, 00°39′10″S, 76°26′00″W, 220 m; terra firma forest, flowerfall, litter, at night; T.L. Erwin, G.E. Ball & D. Shpeley; 5&8.X.1995; 07-95, T.L. Erwin Ecuador Expedition 1995", USNM.

Type Locality.—As given for holotype.

Range.—Ecuador (Fig. 15).

Recognitory Diagnosis.—Distinguished by its large size, smooth pronotum and subdepressed form.

Description.—Large sized, overall length 8.5 mm. Very shiny with brilliant metallic luster, head and pronotum dark virescent, elytra cupreous. Ventral body surface dark brunneous; legs, mouthparts and antennae slightly paler.

Head. Ocular ratio 1.63. Mentum tooth emarginate at apex. Microsculpture of head faint, reticulate; frontal impressions sharp, parallel.

Thorax. Pronotum (Fig. 25F) sinuate to base, basolateral region convex, apex broad, front angles not produced, hind angles denticulate; pronotal basolateral bead broad, sharply narrowed near base; margins paler than disc; basolateral margin not bordered; pronotal microsculpture mesh pattern transverse, very faint, shiny. Basal section of elytral stria 1 present; mesepisternal angle slightly produced as small rounded tubercle; elytral humeral tooth anterad interval 8; microsculpture faint, transverse; intervals slightly convex, intervals 2–3 of equal width. Metacoxal sulcus arcuate, ended medially in coxa.

Abdomen. Abdominal sulci complete, deeply and finely engraved. Male genitalia and female genitalia and reproductive tract not studied.

Etymology.—Specific epithet is a Latin adjective referring to the color contrast between the elytra and forebody.

(15)*Abaris nobilis*, **new species**
Fig. 15, 25G

Type Material.—HOLOTYPE. Female, labeled: "Brazil, Pará: 5 km E Belém, Soil-litter layer in primary "terra firma" forest. June 6:1973, R.T.Schuh", AMNH.

Type Locality.—As given for holotype.

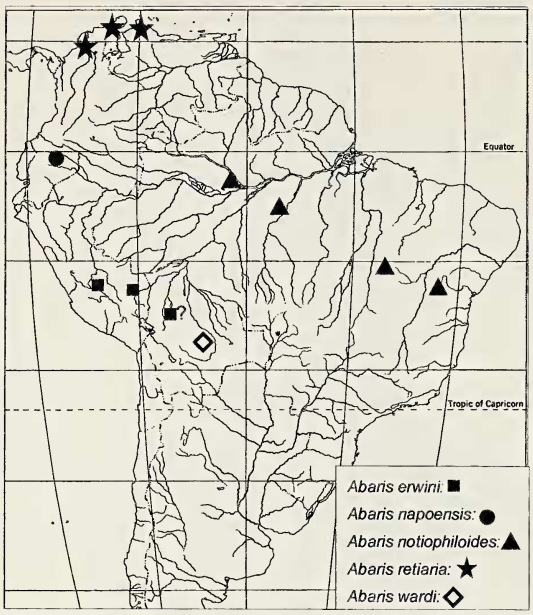

Fig. 11.—Locations of collecting sites for *Abaris* species specimens in South America.

Range.—Brazil (Fig. 15).

Recognitory Diagnosis.—Distinctive species. Largest member of the genus, bright coppery color and arcuate pronotal margins readily distinguishes this species from all others.

Description.—Large size, overall length 8.9 mm. Cupreous throughout; ventral body surface, labrum and mandibles piceous; legs antennae and palpi brunneous.

Head. Eyes relatively small, ocular ratio 1.65. Frontal impressions deep, short, divergent. Mentum tooth deeply emarginate at apex. Microsculpture of head very faint, reticulate.

Thorax. Pronotal (Fig. 25G) basolateral region convex, apex broad, front angles slightly produced, hind angles denticulate, lateral bead broad narrowed to base, basolateral margin not bordered; pronotal microsculpture transverse, very faint, surface shiny. Microsculpture of elytra transverse; basal section of stria 1 present, intervals convex, intervals 2–3 of equal width; humeral tooth anterad interval 8. Mesepisternal angle produced as rounded tubercle. Metacoxal sulcus arcuate.

Abdomen. Sterna V–VI with complete transverse sulci. Male genitalia and female genitalia and reproductive track not studied.

Etymology.—The specific epithet is the Latin adjective *nobilis* (noble) referring to the large size and brilliant copper color of holotype, making it a noble looking animal.

A. tachypoides-group

Cladistic Diagnosis.—All members of this clade share a derived form of the metacoxal sulcus. The metacoxal sulcus is straight and appressed to the apical coxal margin (Fig. 3B, Fig. 32: character 6). The basal grade species, *A. nitida*, *A. franiai* and *A. inflata*, are relatively large and somewhat or quite convex in form. They are similar to *A. bicolor* but have the distinctive straight metacoxal sulcus, not the arcuate condition of *A. bicolor*. The male and female reproductive structures have not been studied for these species. All three species have complete transverse sternal sulci, as does the more apically placed *A. tachypoides*. However,

Fig. 12.—Locations of collecting sites in Central America for *Abaris* species specimens. A. *A. aquilonaria* n.sp. B. *A. bigenera* Bates.

A. tachypoides is much smaller, and has a very different general form than any of these species.

The mid-grade species, *A. tachypoides, A. convexa, A. nigra* and *A. inaequaloides*, are small, have rather narrow pronota with constricted apices. In general, their form somewhat resembles ants or lachnophorine ground beetles.

(16)*Abaris nitida*, **new species**
Fig. 13, 25H

Type Material.—HOLOTYPE. Male, labeled: "Ecuador, Napo, Limoncocha, 100 m, H. Frania, Apr 13–24:1979, Swamp Forest, leaf litter", USNM. ALLOTYPE. Female, labeled: "Ecuador, Napo, Yasuni Scientific Station, 0°40′36″S, 76°24′2″W, 210 m, K.Will, 24:IV:1998", CUIC.

Type Locality.—As given for holotype.

Range.—Ecuador (Fig. 13).

Recognitory Diagnosis.—Distinguished from other member of the group by convex form, deep basal foveae and general form of the pronotum (Fig. 25H).

Description.—Medium sized, overall length 6.7–7.1 mm. Shiny bright aeneous elytra; head and

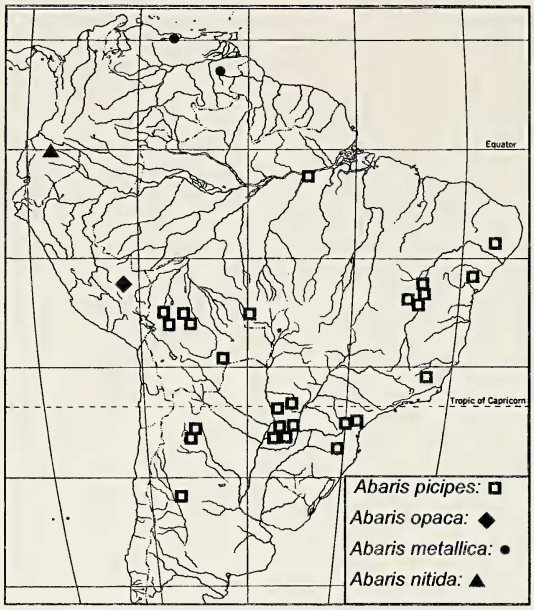

Fig. 13.—Locations of collecting sites for *Abaris* species specimens in South America.

pronotum darker, slightly virescent. Ventral body surface brunneous; mouthparts, antennae and legs paler, ferrugino-testaceous; femora either concolorous with ventral body surface or paler.

Head. Relatively large, ocular ratio 1.67–1.72. Mentum tooth flat and broad at apex, form simple. Head smooth throughout, microsculpture obsolete. Frontal impressions moderately deep, slightly divergent, not delimited medially.

Thorax. Pronotum (Fig. 25H) microsculpture faint, transverse; form very convex, narrow at apex, front angles scarcely produced, lateral bead thick, widened in basal third and narrowed just before denticulate hind angles. Basal section of elytral stria 1 absent; humeral tooth anterad interval 8; microsculpture transverse mesh. Mesepisternal tubercle large. Metacoxal sulcus linear, appressed.

Abdomen. Abdominal sulci complete. Male genitalia and female genitalia and reproductive tract unstudied.

Notes on Life History.—Collected in April at 100–210 m elevation. The Limoncocha specimen was collected in a swamp forest from leaf litter and the Yasuni specimen was collected while using a headlamp and searching leaf litter along a trail in terra firme forest.

Etymology.—The specific epithet is a Latin adjective referring to the shiny appearance of these beetles.

(17)*Abaris franiai*, **new species**
Fig. 16, 26A

Type Material.—HOLOTYPE. Male, labeled: "Bolivia, Cochabamba, Villa Tunari, For. leaf litter, 430 m, May 9:1979, H. Frania", USNM.

Type Locality.—As given for holotype.

Range.—Bolivia (Fig. 16).

Recognitory Diagnosis.—Relatively large and robust form with a relatively broad head. Similar to *A. inflata* and *A. nitida* and must be separated from these by the characters given in the key, e.g., the impunctate pronotal base and sulcate sterna.

Fig. 14.—Locations of collecting sites for *Abaris* species specimens in South America.

Description.—Large sized, overall length 7.9 mm. Aeneous, head and pronotum virescent. Ventral body surface, labrum and mandibles brunneous; legs, palpi and antennae paler.

Head. Ocular ratio 1.89. Mentum tooth form simple. Microsculpture of head faint, reticulate; frontal impressions short, sharply divergent; clypeus with setigerous punctures surrounded laterally by depressions.

Thorax. Pronotal (Fig. 26A) basolateral region slightly convex, apex broad, front angles slightly produced, hind angles with small denticle, lateral bead broad and narrowed to base, basolateral margin not bordered; microsculpture transverse, faint mesh, surface shiny. Microsculpture of elytra transverse; basal section of stria 1 absent, intervals convex, intervals 2–3 of equal width; elytral humeral tooth anterad interval 7. Mesepisternal angle produced as small sharp tubercle. Metacoxal sulcus linear, appressed.

Abdomen. Sternal sulci complete. Male genitalia and female genitalia and reproductive tract unstudied.

Etymology.—Specific epithet is an eponym based on the surname of the collector H. Frania.

(18)*Abaris inflata*, new species
Fig. 16, 26B

Type Material.—HOLOTYPE. Male, labeled: "Bolivia, Cochabamba, Chapare Alto Pol. mar, XI: 1960" [handwritten], MSNM [Straneo Collection].

Type Locality.—As given for holotype.

Range.—Bolivia (Fig. 16).

Recognitory Diagnosis.—Relatively large species, very convex with the pronotum broad.

Description.—Large sized, overall length 7.5 mm. Moderately shiny; elytra with aeneous luster, head and pronotum slightly darker. Ventral body surface, coxae and trochanters brunneous; remaining leg segments, mouthparts and antennae paler.

Head. Relatively broad, ocular ratio 1.78. Mentum tooth form simple, apex broadly rounded. Microsculpture of head obsolete, frontal impressions short, not delimited medially. Clypeus tumescent near frontal suture and depressed near apex.

Thorax. Pronotum (Fig. 26B) convex, front angles scarcely produced, hind angles about right,

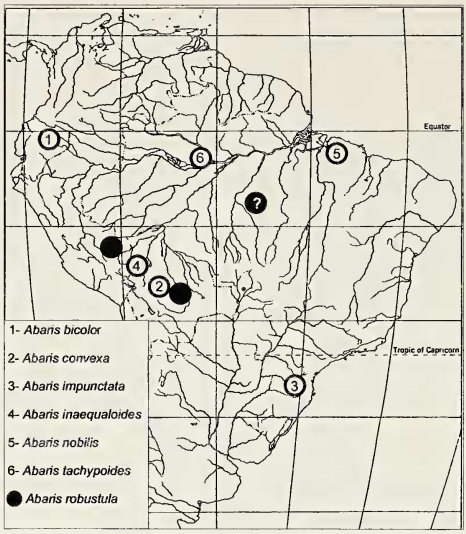

Fig. 15.—Locations of collecting sites for *Abaris* species specimens in South America.

denticulate, lateral bead broad in basal third and sharply narrowed to hind angles, without basolateral border; microsculpture faint and transverse. Elytra basal section of stria 1 absent; mesepisternal angle prominently produced as sharp tubercle, elytral humeral tooth anterad interval 7; microsculpture transverse mesh, intervals 2–3 of equal width. Metacoxal sulcus linear, appressed.

Abdomen. Male genitalia and female genitalia and reproductive tract unstudied.

Etymology.—The Specific epithet is a feminized Latin adjectival of *inflatus* (to blow into) referring to the generally tumescent or robust form of the body.

(19)*Abaris tachypoides* Bates, 1871, **revised combination**
Fig. 9, 15, 21T–U

Abaris tachypoides Bates, 1871:220.

Type Material.—LECTOTYPE (here designated). Male, labeled: "Ega" [handwritten]; "Abaris tachypoides type, Bates" [handwritten]; "Ex Musaeo H.W. Bates, 1892"; "Lectotype, Abaris tachypoides Bates, K.W. Will", MHNP.

Type Locality.—Brazil, Tefé [Ega], from original description.

Range.—Brazil (Fig. 15).

Recognitory Diagnosis.—The relatively large head and narrow pronotum are distinctive (Fig. 9). Similar to *A. inaequaloides*, but distinguished from that species by the straight striae, equal width of elytral intervals and darker, more cupreous body color.

Description.—Small sized, overall length 5.7–6.4 mm. Cupreous, head and pronotum black with slight metallic luster. Ventral body surface, mandibles and labrum brunneous to piceous; legs, palpi and antennae paler ferrugino-testaceous.

Head. Head relatively large, ocular ratio 1.84–1.91. Mentum tooth form simple. Microsculpture of head obscure, reticulate; frontal impressions long, deep, parallel.

Thorax. Pronotal basolateral region convex, apex narrowly constricted, front angles not produced, appressed to occiput, hind angles not denticulate, lateral bead narrow, basolateral margin not bordered; microsculpture on disc reticulate. Elytral microsculpture transverse; basal section of stria 1 absent, intervals convex, intervals 2–3 of equal width; elytral humeral tooth anterad interval 7. Mesepisternal angle produced as small, flat tubercle. Metacoxal sulcus linear, appressed.

Abdomen. Sternal sulci complete, very finely engraved. Basal bulb of male median lobe unmodified

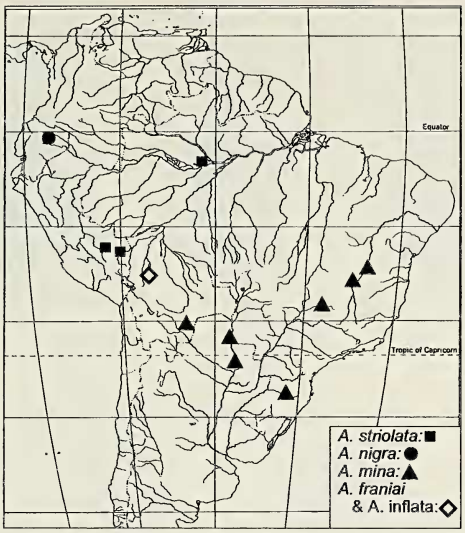

Fig. 16.—Locations of collecting sites for *Abaris* species specimens in South America.

(Fig. 21T–U), endophallus folding pattern not visible, blade smooth (Fig. 21T). Female genitalia and reproductive tract not studied.

Material Examined.—Five specimens examined. **BRAZIL.** Ega [MHNP]; Amazonus [BMNH]. **UNKNOWN:** [BMNH].

(20)*Abaris convexa*, **new species**
Fig. 15, 23G–H, 26C

Type Material.—HOLOTYPE. Male, labeled: "Bolivia, Cochabamba, Villa Tunari, 430 m, H.Frania, inundation for., 9–10:V:1979, rotting flood debris", USNM.

Type Locality.—As given for holotype.

Range.—Bolivia (Fig. 15).

Recognitory Diagnosis.—A small species dorsal surface somewhat dull, more convex in form and with relatively larger eyes than other species of similar size.

Description.—Small sized, overall length 5.4 mm.

Head.—Ocular ratio 1.90. Mentum tooth form simple. Microsculpture of head reticulate; frontal impressions moderately deep, parallel.

Thorax. Pronotal (Fig. 26C) basolateral region convex, apex narrow; front angles not appressed to occiput, not produced; lateral margins subsinuate, hind angles not denticulate, lateral bead uniformly thick, basolateral margin not bordered; microsculpture obvious, reticulate mesh, surface dull. Microsculpture of elytra distinct, transverse; basal section of stria 1 absent, mesepisternal angle produced as small flat tubercle, elytral humeral tooth anterad interval 7. Metacoxal sulcus linear, appressed.

Abdomen. Sterna without sulci. Median lobe (Fig. 23G–H) basal bulb unmodified, endophallus folding pattern not visible; lobe tip (Fig. 23H) bluntly rounded, symmetrical. Female genitalia and reproductive tract unstudied.

Etymology.—Specific epithet is a Latin adjective referring to the convex form of this species.

(21)*Abaris nigra*, **new species**
Fig. 16, 20B, 23I–J, 26D

Type Material.—HOLOTYPE. Female, labeled: "Ecuador, Napo Prov., Tena, Misahualli Hotel Jungle Lodge. 30:I:1999. Italo Tapia", CUIC. ALLOTYPE. Male, same data as holotype, CUIC. PARATYPES: Female, same data as holotype, UASM; Male same data as holotype, QCAZ; Female, labeled: "Ecuador, Napo, Anaconda Lodge, Napo River, D. Brzoska, 14:II:1991", SEMC.

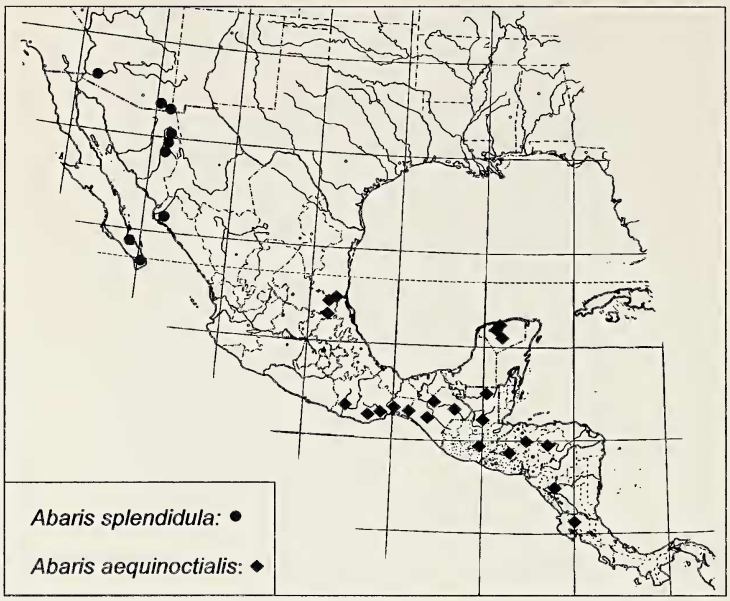

Fig. 17.—Locations of collecting sites for *Abaris* species specimens in southern North America and Central America.

Type Locality.—As given for holotype.

Range.—Ecuador (Fig. 16).

Recognitory Diagnosis.—The dark bronze-black color, bicolored legs, and rounded humeral angles set this species apart from all others. Somewhat similar to *A. inaequaloides*, but front angles not tight to occiput as in that species.

Description.—Small sized slightly built, overall length 6.0–6.2 mm. Black with bronze luster. Ventral body surface black; legs, except femora, mouthparts and antennae brunneous with darker infuscation; femora flavotestaceous, distinctly contrasted with ventral surface, only darker near base.

Head. Ocular ratio 1.74–1.80. Mentum tooth form simple. Microsculpture of head reticulate; frontal impressions deep, divergent, not clearly delimited medially.

Thorax. Pronotal (Fig. 26D) basolateral region convex, apex narrow, front angles not produced, lateral margins sinuate, hind angles not denticulate, lateral bead narrow and uniformly thick, basolateral margin not bordered; microsculpture on disc reticulate, distinct mesh, surface dull. Elytral microsculpture transverse; basal section of stria 1 absent; intervals slightly convex, flatter on disc; intervals 2–3 of equal width, both widened medially; stria 3 sinuate in basal quarter; elytral humeral tooth anterad interval 7. Mesepisternal angle produced as very small, sharp tubercle. Metacoxal sulcus linear, appressed.

Abdomen. Sterna without sulci. Median lobe (Fig. 23I–J) basal bulb unmodified, endophallus folding pattern visible in cleared lobe, blade (Fig. 23I) smooth. Female reproductive tract with broad, straight seminal canal, receptaculum large, distinct, spermatheca with a large basal expansion, appended gland spherical; gonocoxite-1 with 2 apicolateral ensiform setae.

Notes on Life History.—Specimens have been collected in January and February. The Misahualli site was sampled in April, May and October as well, and no *A. nigra* were found during these months. The habitat in the area of the type locality is terra firme forest that is mostly secondary growth mixed with small plots of primary forest.

Material Examined.—Six specimens examined. In addition to the type material, a single male with the same data as the holotype was preserved in 100% EtOH, KWWC.

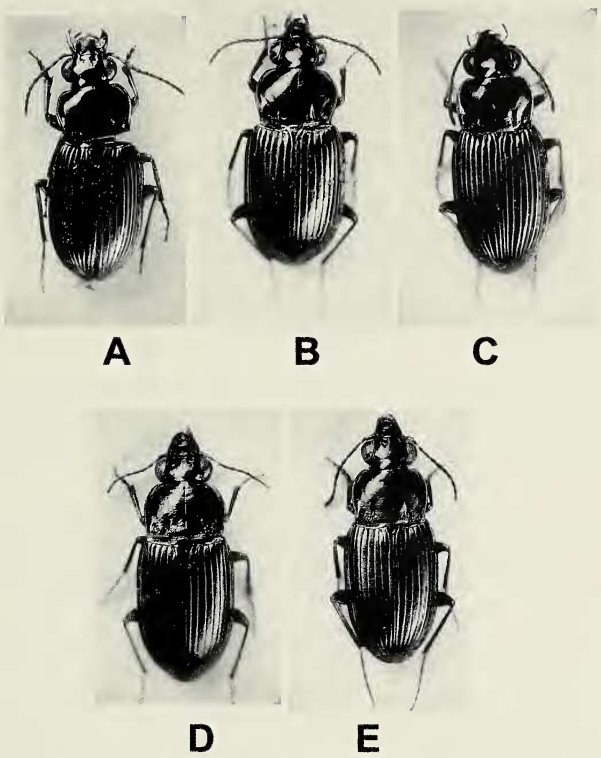

Fig. 18.—Photographs of dorsal view of *Abaris* species. A. *A. napoensis* n.sp. B. *A. erwini* n.sp. C. *A. aenea* Dejean. D. *A. picipes* Bates. E. *A. basistriata* Chaudoir.

Etymology.—Specific epithet is a Latin adjective referring to black body color in this species.

(22)*Abaris inaequaloides*, **new species**
Fig. 15, 26E

Type Material.—HOLOTYPE. Female, labeled: "Bolivia, Beni, Cercado, 1 km N Ballivian, Río Ibare, 14°47′S, 64°59′W, 124 m, 3 Apr 1994, R.Ward", CMNH.

Type Locality.—As given for holotype.

Range.—Bolivia (Fig. 15).

Recognitory Diagnosis.—Very distinctive species, at once recognized by the reticulate microsculpture, dull dorsal surface, bronze color and narrow pronotum relative to the large head.

Description.—Medium sized, overall length 6.3 mm. Head and pronotum dull, elytra moderately shiny, bronze luster throughout. Ventral body surface, coxae and trochanters brunneous; remaining leg segments, mouthparts and antennae paler, flavotestaceous.

Head. Relatively large, ocular ratio 1.85. Mentum tooth form simple. Microsculpture of head pronounced, reticulate; surface finely strigate laterad frontal impressions. Frontal impressions short, parallel and moderately deep.

Thorax. Pronotum (Fig. 26E) relatively narrow, basolateral region convex, front angles rounded, not at all produced, hind angles obtuse, not denticulate, lateral bead narrow uniformly thick, laterobasal margin not bordered; microsculpture reticulate mesh; surface dull. Elytra shiny, microsculpture reticulate mesh; basal section of stria 1 absent, interval 3 width 1.7× interval 2, dorsal punctures foveate,

striae 4–5 slightly sinuate in basal third; humeral tooth anterad interval 7. Mesepisternal angle slightly produced, broad and rounded. Metacoxal sulcus linear, appressed.

Abdomen. Sterna without sulci. Male genitalia and female genitalia and reproductive tract unstudied.

Etymology.—Specific epithet is Latinized adjective refering to this species' general similarity to species of the *B. inaequale*-group of the genus *Bembidion* Latreille, 1802.

(23)*Abaris opaca*, new species
Fig. 13, 26F

Type Material.—HOLOTYPE. Female, labeled: "Peru, Madre de Dios, Tambopata Res. Zone, Explorer's Inn, 12°50′S, 69°17′W, Fig fall, at night, Río La Torre to Sunset Point trail, 1 Nov 1982, 290 m, T.L.Erwin and L.Sims", USNM.

Type Locality.—As given for holotype.

Range.—Peru (Fig. 13).

Recognitory Diagnosis.—Black species with reticulate microsculpture on dorsum. Very similar to *A. wardi* but with the mentum tooth form broad and slightly emarginate at the apex. Pronotal apex narrow but angles not appressed to occiput as in *A. inaequaloides*.

Description.—Medium sized, overall length 6.5 mm. Black with aeneous luster, less pronounced on head and pronotum. Ventral body surface piceous; legs, mouthparts and antennae brunneous.

Head. Ocular ratio 1.89. Mentum tooth form broad, and emarginate at apex. Microsculpture on head reticulate mesh; frontal impressions shallow, sharp, slightly divergent, not clearly delimited medially.

Thorax. Pronotal basolateral region convex, apex narrow; hind angles very slightly obtuse to right angled, not denticulate; lateral bead uniformly thick, basolateral margin not bordered; obvious microsculpture on disc, reticulate; surface dull. Microsculpture of elytra reticulate; basal section of stria 1 absent, intervals slightly convex, interval 3 width 1.4× interval 2, humeral tooth anterad interval 8. Mesepisternal angle barely produced, not tuberculate. Metacoxal sulcus linear, appressed.

Abdomen. Sterna without sulci. Male genitalia and female genitalia and reproductive tract unstudied.

Etymology.—Specific epithet is a Latin adjective referring to the dull of the dorsal surface.

(24)*Abaris splendidula* (LeConte, 1863)
Fig. 1, 7A–C, 17, 23K–L, 27B

Pterostichus spendidulus LeConte, 1863:10. Abaris splendidula: redescription (Bousquet 1984:384).

Type Material.—HOLOTYPE. Female, labeled: [round label with yellow= western states]; "979"; "Type 5648"; "Pterostichus splendidulus Lec."; "J.LeConte collection; Abaris splendidula (LeC.) Det. 1982, Y.Bousquet", MCZC. Redescribed by Bousquet (1984).

Type Locality.—Fort Yuma, California, from original description.

Range.—Mexico, southwestern USA (Fig. 17).

Recognitory Diagnosis.—Moderately shiny with a convex form and flat elytral intervals. No other *Abaris* species is known from the region inhabited by *A. splendidula*.

Description.—Small sized, overall length 5.4–6.5 mm. Black with a cupreous or virescent luster. Ventral body surface, mandibles and labrum rufopiceous; legs, palpi and antennae ferruginous.

Head. Ocular ratio 1.75–1.86. Mentum tooth form simple. Microsculpture of head reticulate; frontal impressions deep, sharply delimited laterally, obscurely so medially.

Thorax. Pronotal (Fig. 27B) basolateral region convex, apex broad, front angles not produced, margins subsinuate, hind angles not denticulate, lateral bead narrow and uniformly thick, basolateral margin bordered; microsculpture transverse. Microsculpture of elytra reticulate, obvious; basal section of stria 1 absent, intervals flat, intervals 2–3 of equal width, humeral tooth anterad interval 8. Mesepisternal angle produced as a very small round tubercle. Metacoxal sulcus linear, appressed. Hind wing as in figure 7C.

Abdomen. Sterna without sulci. Pygidial gland system as in figure 7A. Alimentary tract as in figure 7B. Basal bulb of male median lobe (Fig. 23K–L) unmodified, endophallus folding pattern not visible; blade smooth (Fig. 23K). Female reproductive tract seminal canal narrow with few tight twists along

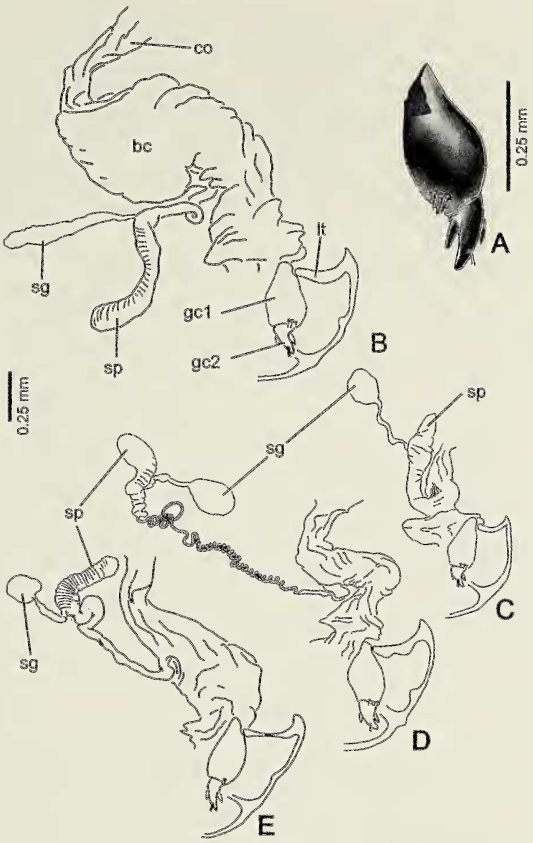

Fig. 19.—*Abaris* species female reproductive tract and genitalic features of *A. napoensis* n. sp. A. Ventral view of right gonocoxite. B. Ventral view of reproductive tract and genitalia, right gonocoxite removed. Same for C. *A. notiophiloides* Bates. D. *A. bigenera* Bates. E. *A. picipes* Bates. Scale for B, C, D and E at left. Legend: bc, bursa copulatrix; co, common oviduct; gc1, basal gonocoxite; gc2, apical gonocoxite; lt, laterotergite IX; sg, appended gland of spermatheca; sp, spermatheca.

length, receptaculum distinct, appended gland spherical; gonocoxite-1 with 1 apicolateral ensiform seta.

Notes on Life History.—Bousquet (1984) cited comments by G. E. Ball on the situation in which *A. splendidula* was collected in Mexico. Specimens were collected "in thin leaf litter, on damp sandy-clay spots in open woodland dominated by acacias and on the flood plain of a riparian forest." Two specimens I collected in Arizona, USA in November were found by raking *Salix* leaf litter on sandy soil along the Santa Cruz River. I collected many additional specimens in various sites in Arizona in July and August in similar situations along washes with or without water present. Individuals were generally 1–3 meters back from the main erosion channel in semi-shaded areas with ample leaf litter. Some activity was observed in late afternoon but most beetles were found at night while searching with a headlamp. Two specimens collected at light in Tucson were found at large fluorescent lights at the edge of the city on evenings when it rained either before or just after collecting the beetles. This suggests some relationship between timing of dispersal activity and rain patterns. Adults have been collected in January, July,

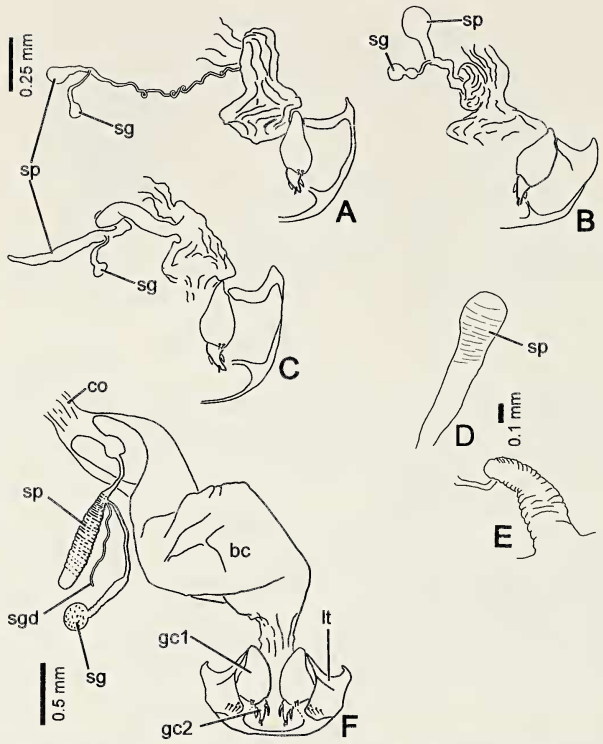

Fig. 20.—Abariform species female reproductive tract and genitalic features of A. *Abaris aquilonaria* n.sp., ventral view of reproductive tract and genitalia, right gonocoxite removed. Same for B. *A. nigra* n.sp. C. *A. aequinoctialis* Chaudoir. D–E. *A. retiaria* n.sp. F. *Pseudabarys* undescribed sp. Ecuador, both gonocoxites shown. Scale for A, B, and C at upper left. Legend: bc, bursa copulatrix; co, common oviduct; gc1, basal gonocoxite; gc2, apical gonocoxite; lt, laterotergite IX; sg, appended gland of spermatheca; sgd, spermathecal gland duct diverticulum; sp, spermatheca.

August and November at elevations from sea level to 1100 m. Data labels include collections in several similar forest types; dry tropical scrub, gallery, riparian, riparian tropical scrub forests. Specimens have been taken in leaf litter and rarely at lights (n = 3).

The male and female collected in Arizona in November were dissected and reproductive organs examined. Neither specimen was in breeding condition, i.e, ovaries were not enlarged and male accessory glands were not turgid. Beetles collected from July to August were kept alive and actively mated producing eggs.

Material Examined.—More than 100 specimens examined. **MEXICO. Baja California Sur Notri:** 18 km S Loreto [UASM]. **Sonora:** 17 km sw Moctezuma rte 21[UASM]; 19.3 km n Imuris Rte 15 [UASM]; 55 km sw Moctezuma rte 21 [UASM]; Fuerte, 18 km n Los Mochis on rte15 [UASM]; Sta. Ana [EMEC].

UNITED STATES. Arizona. Cochise Co.: St. David [UASM]; rt 80 at San Pedro River[KWWC]. **Pima Co.:** 31 km NW Tucson [CMNH]; Arivaca [UASM]; Florida Cyn.Sta Rita Range Res.[UATU]; Green Valley [AMNH]; Waterman Mtns. [UATU]; Baboquivari Mnts, Brown Canyon [KWWC]; Arivaca Wash, Arivaca [KWWC]; Tucson at lights [KWWC]. **Sta. Cruz Co.:** [USNM]; Patagonia [USNM]; Tumacacori at Sta. Cruz River, 31°33′46″N, 111°2′43″W [KWWC].

(25)*Abaris wardi*, **new species**
Fig. 11, 23M–N, 27A

Type Material.—HOLOTYPE. Male, labeled: "Bolivia, Santa Cruz, Ichilo Province, Buena Vista, 400 m R.Ward, 3:X:1994, MV light", CMNH. ALLOTYPE. Female, labeled: "Bolivia, Cochabamba Puerto Villarroel", UASM. PARATYPES. Female, labeled: "Brazil, Cuyaba, Mtt. Grosso", MCZC; Male, labeled: "Bolivia, Sta Helena, W.M.Mann, X, Mulford BioEpl 1921–22", USNM. Male, labeled: "Cetto Verde (S.Ama) Bechyne, 16:V:1969", MSNM. Female, labeled: "Bolivia, Santa Cruz, Province Andres Ibanez Vallecito, 4–5 Oct 1994, R.D.Ward", CMNH.

Type Locality.—As given for holotype.

Range.—Bolivia, Brazil (Fig. 11).

Recognitory Diagnosis.—Medium to small size with obvious, reticulate microsculpture. Very similar to *A. opaca* but separable from that species by the simple form of the mentum tooth. Pronotal apex narrow but front angles not appressed to occiput as in *A. inaequaloides*.

Description.—Medium to small sized, overall length 5.8–7.0 mm. Black with bronze or cupreous luster. Ventral body surface piceous; legs, mouthparts and antennae paler brunneous or rufous.

Head. Ocular ratio 1.74–1.82. Mentum tooth form simple. Microsculpture of head reticulate; frontal impressions long, divergent or sinuate, not clearly delimited medially.

Thorax. Pronotal (Fig. 27A) basolateral region convex, apex narrow, front angles not produced, hind angles not denticulate, lateral bead narrow, basolateral margin not bordered; microsculpture obvious on disc, reticulate; surface dull. Microsculpture of elytra reticulate; basal section of stria 1 absent, intervals convex to almost flat, interval 3 width equal to or up to 1.4× interval 2, elytral humeral tooth anterad interval 8. Mesepisternal angle rounded, not produced. Metacoxal sulcus linear, appressed.

Abdomen. Sterna without sulci. Basal bulb of male median lobe (Fig. 23M–N) unmodified, endophallus folding pattern not visible, lobe smooth, apical blade uniform, straight, thin. Female tract with seminal canal broad, straight, receptaculum not distinct from canal, spermatheca without basal bulb, appended gland spherical; gonocoxites-1 with 3 apicolateral ensiform setae.

Etymology.—Specific epithet is an eponym based on the surname of the collector Robert D. Ward.

(26)*Abaris aequinoctialis* Chaudoir, 1852
Fig. 17, 20C, 23O–P, 26G–H

Abaris aequinoctialis Chaudoir, 1852:76. Abarys aequinoctialis: Chaudoir, 1873:98.

Type Material.—LECTOTYPE, (here designated). Female, labeled: "ex Museo Chaudoir" [red ink]; "Lectotype" [Handwritten on circular label with purple edge]; "Lectotype, Abaris aequinoctialis Chd., Det. G.E.Ball '72", MHNP.

Type Locality.—Temax, Yucatan, Mexico, from original description.

Range.—Mexico, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua (Fig. 17).

Recognitory Diagnosis.—Most common species from southern Mexico and Central America. Similar in form to *A. splendidula* but separable by the transverse microsculpture of the elytra. The known range of *A. aequinoctialis* is not overlapping and south of *A. splendidula* (Fig. 17).

Description.—Small sized, overall length 5.1–6.5 mm. Dorsal surface shiny, virescent or cupreous throughout, or bicolored with head and pronotum darker green and elytra dark cupreous. Ventral body surface rufous; legs and mouthparts paler rufous or ferrugino-testaceous; coxae and femora concolorous with ventral body surface; tibiae and tarsi paler in some individuals, nearly flavescent.

Head. Ocular ratio 1.74–1.88. Mentum tooth form simple. Microsculpture of head faint, reticulate. Clypeus smooth, fronto-clypeal suture evident, frontal impressions short and not clearly delimited medially.

Thorax. Pronotum convex, margins sinuate anterad base and convex laterad basolateral foveae, hind angles slightly obtuse, not denticulate, lateral bead narrow, uniformly thick; microsculpture on disc transverse (microsculpture faint and surface shiny in most specimens from Guatemala and Yucatan,

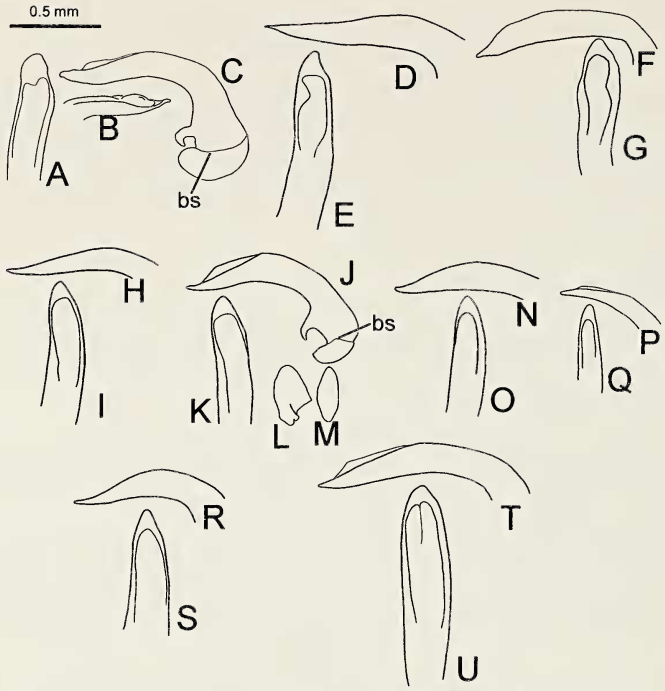

Fig. 21.—Features of male genitalia of *Abaris* species. A, E, G, I, K, O, Q, S, U, dorsal view blade of median lobe; D, F, H, N, P, R, T, right lateral view of blade; C, J, right lateral view of median lobe; B, left lateral view of blade; L, left paramere; M, right paramere. A–C. *A. napoensis* n.sp. D–E. *A. striolata* n.sp. F–G. *A. robustula* Tschitschérine. H–I. *A. aenea* Dejean. J–M. *A. erwini* n.sp. N–O. *A. aquilonaria* n.sp. P–Q. *A. notiophiloides* Bates. R–S. *A. impunctata* n.sp. T–U. *A. tachypoides* Bates. Legend: bs, basal bulb sulcus.

Mexico, obvious mesh in most specimens from other areas). Base of pronotum with or without lateral border (best developed in Yucatan, Mexico specimens). Basal section of elytral stria 1 absent; position of humeral tooth variable either anterad interval 7, stria 7, or barely attaining interval 8; microsculpture transverse; intervals 2–3 subequal.

Abdomen. Sterna without sulci. Blade of median lobe (fig. 23O–P) thin, smooth; tip (Fig. 23P) bluntly rounded, endophallus folding pattern not visible, basal bulb unmodified laterally. Female reproductive tract with seminal canal straight, broad, receptaculum not distinct; appended gland spherical; gonocoxite-1 with 2–3 apicolateral ensiform setae.

Notes on Life History.—Specimens have been collected in all months. Habitat data includes leaf litter of rainforest, coffee finca and palm forest. Specimens were collected at sea level to 1400 m elevation. One record was associated with rotting fruit. Nine specimens were taken at "lights" or Ultraviolet light.

Material Examined.—239 specimens. **COSTA RICA.** unknown [USNM]; Guanacaste Prov.; 3 km N Cañas Hac. La Pacifica [UASM]; 5 km N Cañas [UASM]; Las Cañas [UASM]; Santa Rosa National Park Administ. & Research Center, 150 m [CASC]; 30 km norte de Liberia, Finca Jenny [INBC]; 3 km N de Nacaome, P.N.Barra Honda [INBC]; 8 km S de Caujiniquil, Est. Muriélago [INBC]; Barra Honda, A.C.Tempisque, Los Mesoes [INBC]; Est. Cacao, Lado suroeste del Vol. Cacao [INBC]; Est. Las Pailas, P.N.Rincon de la Vieja [INBC]; Est.Lomas Barbudal, A.C.T. [INBC]; Est.Maritza, Lado oeste del Volcan Orosi [INBC]; Est.Palo Verde, P.N.Palo Verde [INBC]; Est.Sta Rosa, P.N.Guanacaste [INBC]; Ojochal, P.N.Sta. Rosa [INBC]; P.N. Barra Honda [INBC]; Parcelona.Asemtamiento Juan Santamaria [INBC]; Playa Naranjo, P.N.Sta. Rosa [INBC]; Ref.Nac.Fauna Silvestre R.L.Rodriguez [INBC].

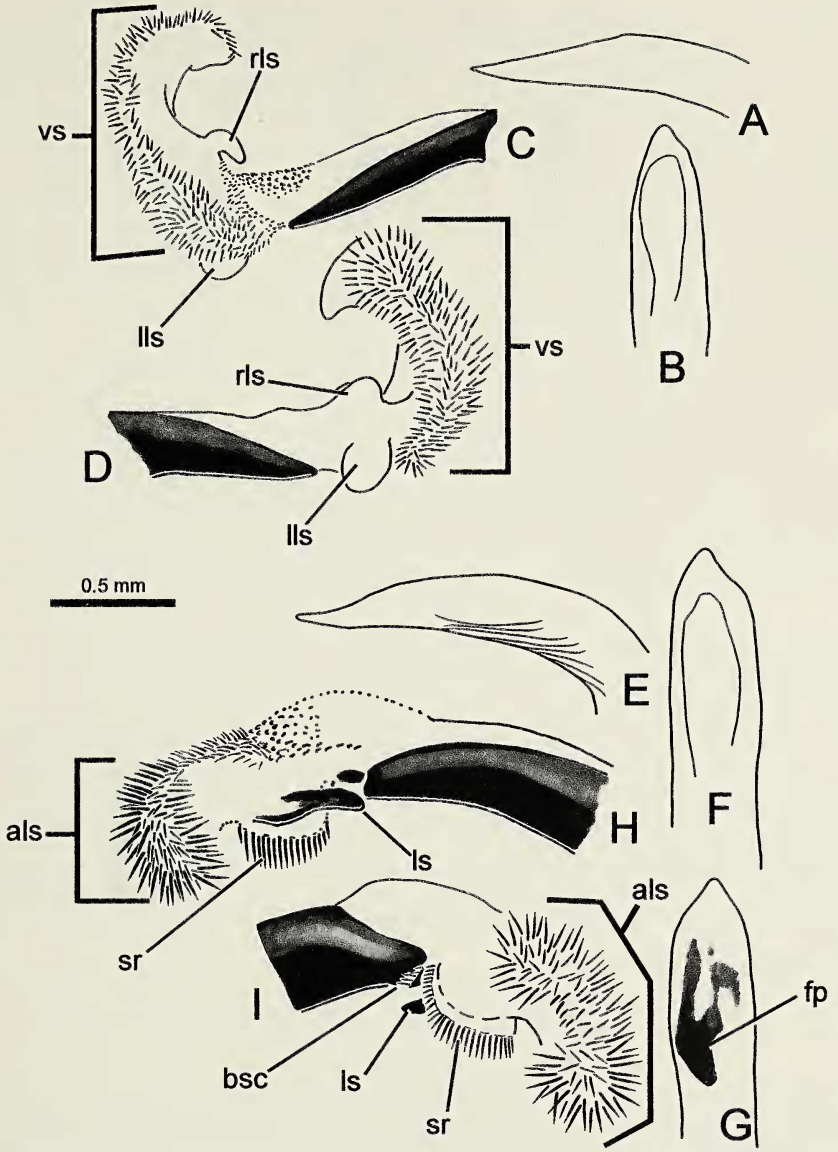

Fig. 22.—Features of male genitalia of *Abaris* species. B, F, dorsal view blade of median lobe; A, E, right lateral view of blade; G, ventral view of blade; C, H, right lateral view tip of median lobe and everted endophallus; D, I, left lateral view tip of median lobe and everted endophallus. A–D. *A. bigenera* Bates. E–I. *A. basistriata* Chaudoir. Legend: als, anterior spine field; bsc, basal scale; fp, folding pattern of endophallus; lls, left lateral sacculus; ls, lateral scale; rls, right lateral sacculus; sr, spine row; vs, ventral spine field.

EL SALVADOR. Isalco [USNM]; Sta. Anna, 6 km W Hwy.CA1, above Lago de Coatepeque, [USNM].

GUATEMALA. 250 km N San Felipe [BPBM]; Tikal [BPBM, RSCI]; Tikal Rainforest, [UASM]; Zapote [MCZC, MHNP]; El Progreso, 6 km E San Cristobal, Acasaguastlan [USNM]; Peten, Tikal [USNM, UASM].

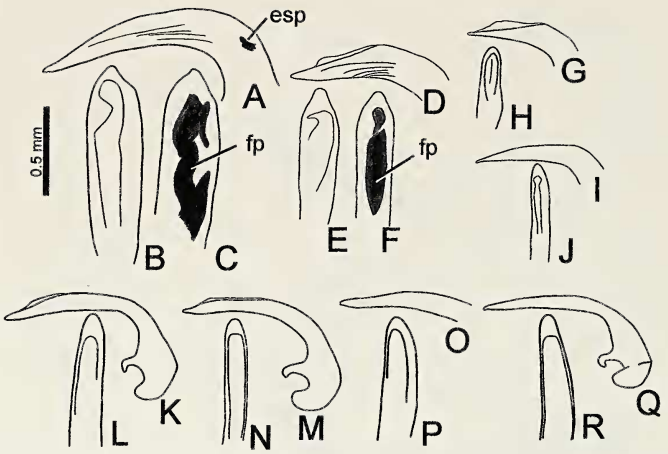

Fig. 23.—Features of *Abaris* species male genitalia. B, E, H, J, L, N, P, R, dorsal view blade of median lobe; A, D, G, I, O, right lateral view of blade; C, F, ventral view of blade; K, M, Q, right lateral view of median lobe. A–C. *A. picipes* Bates. D–F. *A. mina* n.sp. G–H. *A. convexa* n.sp. I–J. *A. nigra* n.sp. K–L. *A. splendidula* (LeConte). M–N. *A. wardi* n.sp. O–P. *A. aequinoctialis* Chaudoir. Q–R. *A. retiaria* n.sp. Legend: esp, endophallus spine patch; fp, endophallus folding pattern.

HONDURAS. [MHNP]; Honduras, Copán, Ruinas de Copán [UMMZ]; Morazán, Esc. Agr. Pan. Zamorano [UMMZ]; Francisco, Zamorano, 47°0′N–80°0′W [SEMC].

MEXICO. unknown [MHNP]← Paz, V.San Yicente Finca, J.Bechyne [MHNP]; 18 mi. N San Andre V [MHNP]. **Chiapas:** 32.5 mi. E Comitan, Rte190 [UASM]; 4.9 mi. N Frontera Comalapa, 727 m; 7.7 mi. N Frontera Comalapa [UASM]; 5.3 mi. S Union Juárez; Cinco Cerros; Cinco Cerros, km30 on Hwy190 [UASM]; El Aguacero,16 km W Ocozocuautla [UASM]; Trinitaria [UASM]; Puente Macuilapa nr. Los Amates [CASC]. **Hildalgo:** 7 mi. NE Jacala [OSUC]. **Oaxaca:** 5.0 mi. E Tapanatepec, rte190 [UASM]; 7.6 mi. W Zanatepec, rte190 [UASM]; Río Miltepec 18.4 mi. W Zanatepec, rte190 [UASM]; Hy200 km194 E Puerto Angel [AMNH]. **San Luis Potosí:** 1.8 mi. N El Naranjo [UASM]; El Salto de Agura [CNC]; El Salto de Agura, 7 mi. N El Naranjo [UASM]. **Tamulipas:** 1.4 mi. SE Chamal [UASM]. **Yucatán:** 12 km N Piste [UASM];2 km E Chichen Itza [UASM]; Chuminopolis [AMNH]; Tehuantepec [AMNH]; Temax [MHNP]; Zopilote, 1.5 mi. E nr.Pan Am. Hyw. [UASM].

NICARAGUA. Chontales [MHNP].

(27)*Abaris retiaria*, new species
Fig. 11, 20D–E, 23Q–R, 27C

Type Material.—HOLOTYPE. Male, labeled: "Venezuela, Falcon, Paraguana Pen S Jose Cueva Piedra Honda, 100 m, S.Peck, 3:III:1971", USNM. ALLOTYPE. Female, labeled: "Colombia, Magdalena, Rio Frio, P.J.Darlington, 1:XI:1928", MCZC. PARATYPES. Female, label data same as allotype, MSNM. Male, label data same as allotype, MCZC. 3 females, label data same as allotype except date Sept, XI and VIII respectively, MCZC. Female, labeled: "Venezuela, Buena Vista Paraguana, Falcon, Bordon, 2:I:1971", BORD. Male, labeled: "Venezuela, Maracaibo", USNM.

Type Locality.—As given for holotype.

Range.—Colombia, Venezuela (Fig. 11).

Recognitory Diagnosis.—Easily recognized from all other species by the obvious reticulate mesh microsculpture, square form and bordered base of the pronotum.

Description.—Small sized, overall length 5.1–5.8 mm. Brunneous with a cupreous or virescent luster. Ventral body surface, legs and mouthparts paler.

Head. Ocular ratio 1.64–1.75. Mentum tooth form simple. Microsculpture obvious on head, reticulate; frontal impressions sharp, divergent, clypeus finely strigate.

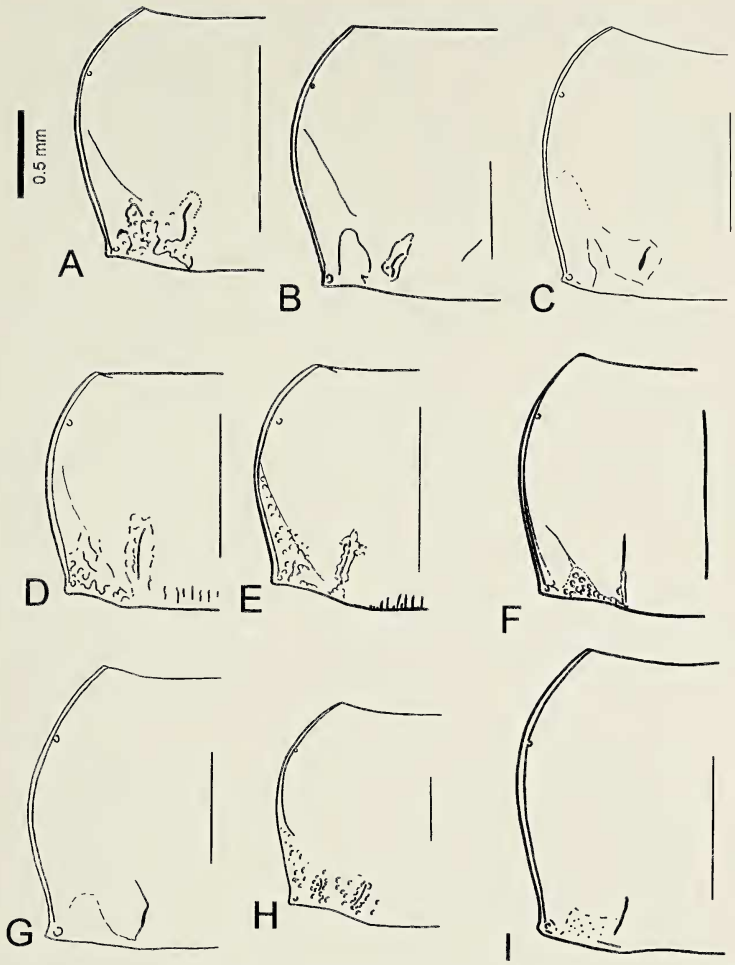

Fig. 24.—Pronota of *Abaris* species. A. *A. napoensis* n.sp. B. *A. striolata*. C. *A. robustula* Tschitschérine. D. *A. aenea* Dejean, smooth form. E. Same, punctate form. F. *A. erwini* n.sp. G. *A. aquilonaria* n.sp. H. *A. notiophiloides* Bates. I. *A. impunctata* n.sp.

Thorax. Pronotal (Fig. 27C) basolateral region slightly convex, apex broad, front angles produced, lateral margins straight, hind angles obtuse, not denticulate; pronotal lateral bead uniformly thick, continuous laterally on base; microsculpture obvious, reticulate, dull. Elytral microsculpture reticulate; basal section of stria 1 absent, intervals little convex, intervals 2–3 of equal width, elytral humeral tooth anterad interval 8. Metacoxal sulcus linear, appressed to apical margin of coxae. Mesepisternal angles produced as low tubercle.

Abdomen. Sterna without sulci. Basal bulb of male median lobe (Fig. 23Q) unmodified, endophallus folding pattern not visible; median lobe straight, smooth; tip (Fig. 23R) evenly rounded. Female tract with seminal canal broad, straight, receptaculum not discrete, spermatheca with basal bulb, appended gland unknown (Fig. 20D–E); gonocoxite-1 with 2 apicolateral ensiform setae. (Because all female specimens were collected into very strong EtOH by P.J. Darlington, female tracts could not be removed without damage. Therefore, this description is based on the fragments of the attempted dissections and may require subsequent revision.)

Etymology.—Specific epithet is a feminized noun in apposition based on the Latin *Retiarius* (type of Roman gladiator bearing a net to entangle his adversary). This calls attention to the net-like reticulate mesh of microsculpture on the pronotum.

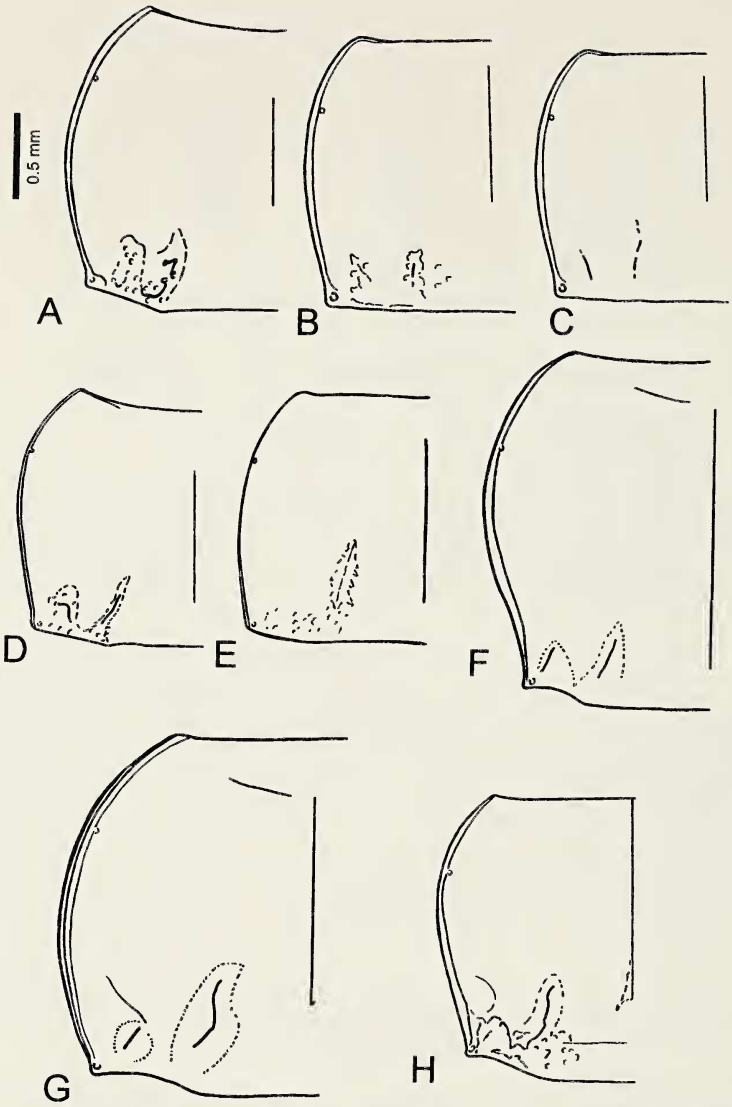

Fig. 25.—Pronota of *Abaris* species. A. *A. bigenera* Bates. B. *A. picipes* Bates. C. *A. mina* n.sp. D. *A. basistriata* Chaudoir. E. *A. metallica* n.sp. F. *A. bicolor* n.sp. G. *A. nobilis* n.sp. H. *A. nitida* n.sp.

Cladistic Analysis

Outgroup Selection

Three genera, *Orthomus, Prosopogmus,* and *Pseudabarys*, were used as outgroups in this analysis. They were selected from among 115 genera examined as the basis of the analysis of pterostichine taxa (Will, 2000). All three outgroups plus *Neotalus* and *Abaris* comprise a taxon characterized by a "gooseneck" shaped bursa of the female reproductive tract (e.g., Fig. 19B, 20F). *Orthomus, Pseudabarys* and *Abaris* share a reduced or absent coronal suture in the larvae (Bousquet and Liebherr, 1994; Will, 2000). *Prosopogmus* adults are very similar

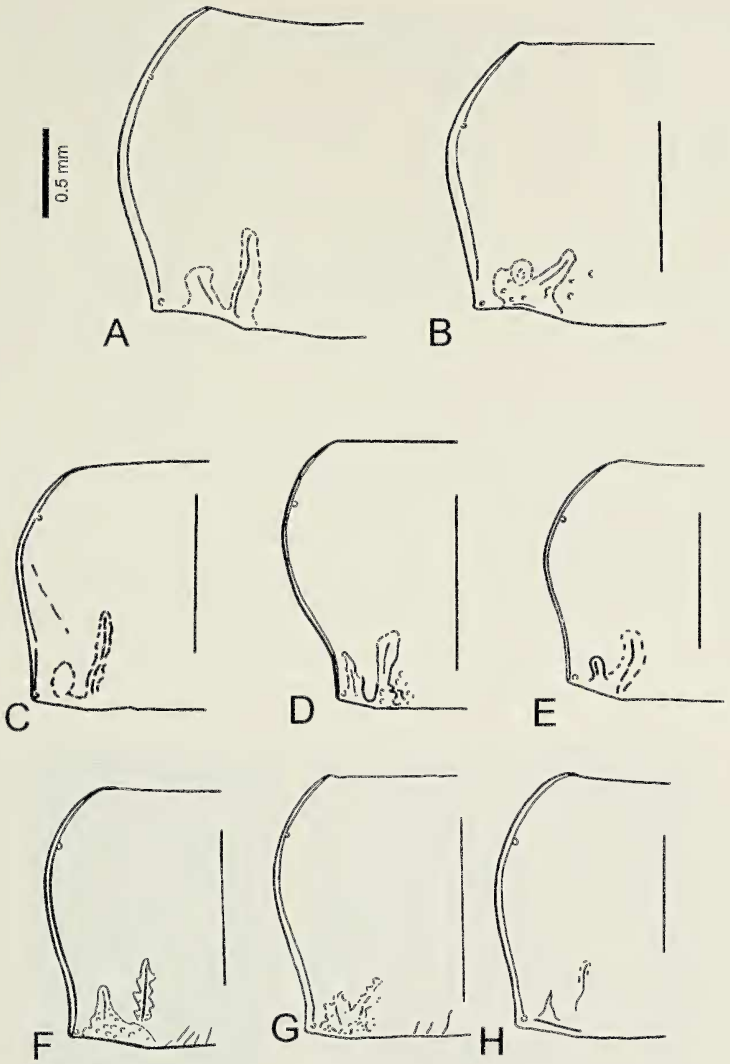

Fig. 26.—Pronota of *Abaris* species. A. *A. frania* n.sp. B. *A. inflata* n.sp. C. *A. convexa* n.sp. D. *A. nigra* n.sp. E. *A. inaequaloides* n.sp. F. *A. opaca* n.sp. G. *A. aequinoctialis* Chaudoir, punctate form, Chiapas, Mexico. H. Same, smooth and basally bordered form, Guatemala.

in general form to some *Abaris* species and *Pseudabarys* shares the paired dorsal bursal glands with *Neotalus* and *Abaris*. Although some of the relationships hypothesized in my higher level analysis (Will, 2000) are not found in the consensus of all most parsimonious cladograms, the set of relationships (*Orthomus* (*Prosopogmus* (*Pseudabarys* (*Neotalus* + *Abaris*)))) is supported under every resolution in the full character analysis. Therefore, rooting between *Orthomus* and the remaining taxa is clearly justified.

Character List

1. Maxillary palpomere 3: greater than half length of paplpomere 4 (Fig. 28A) (0); less than half length of palpomere 4 (Fig. 28B) (1).

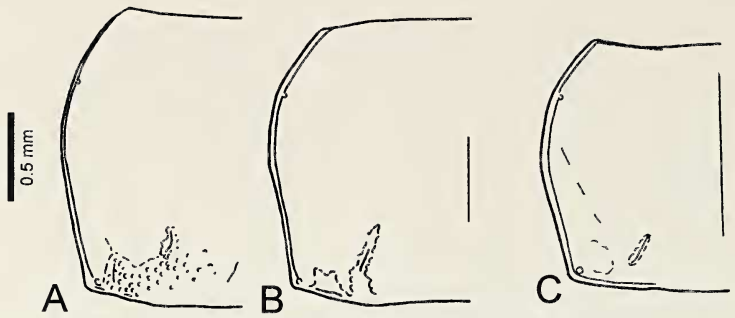

Fig. 27.—Pronota of *Abaris* species. A. *A. wardi* n.sp. B. *A. splendidula* (LeConte). C. *A. retiaria* n.sp.

2. Ocular ratio, measured as width across eyes/width between eyes at level of anterior supraorbital setae (Fig. 29). Less than 1.55 (0); Greater than 1.60 (1). Measurements of ocular ratio were taken to determine if a discrete gap existed between clusters of measurements. Species with similarly developed eyes could then be coded as having the same character state. Measurements of three individuals per species were taken if specimens were available. This ratio was plotted and a gap between 1.55 and 1.60 was found and used to establish states. Figure 29 shows a plot of the measurements and indicates the gap between states.

3. Mentum tooth apex emarginate (0); simple, not emarginate (1).

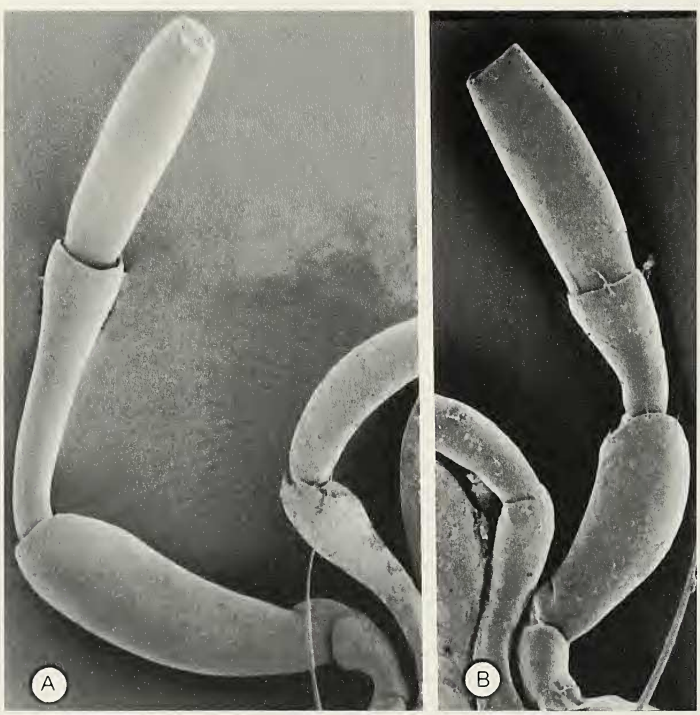

Fig. 28.—Scanning electron micrograph, ventral view. A. Right maxillary palpi *Lophoglossus scrutator* (LeConte) Pterostichini. B. Left maxillary palpi *Abaris aenea* Dejean.

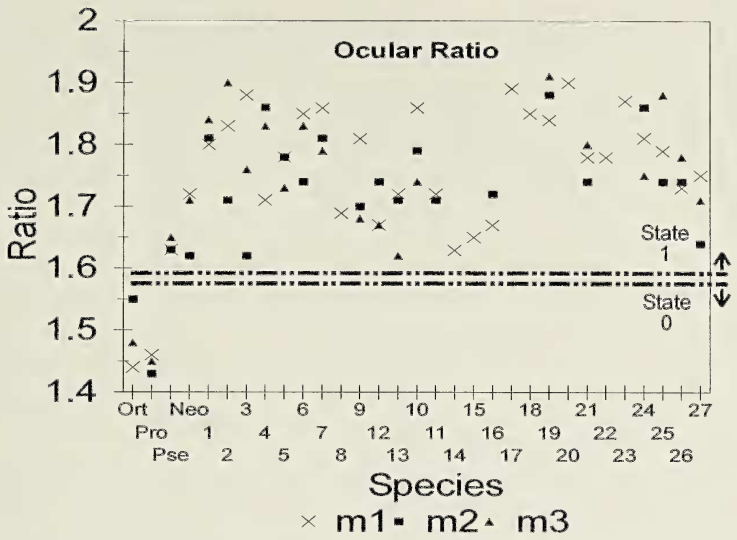

Fig. 29.—Graph of ocular ratio measurements showing separation of states for the character. Up to three measurements were taken for each species. Legend: m1, m2, m3, measurements; Ort, *Orthomus*; Pro, *Prosopogmus*; Pse, *Pseudabarys*; Neo, *Neotalus*; Numbers 1–27 correspond to *Abaris* species numbers in the text.

4. Reticulate microsculpture on vertex of head. Very faint but visible in clean specimens (0); obsolete (1).

5. Micropunctulae present on vertex of head (0); absent (1). These punctures are small (visible at 25× or greater) and irregularly scattered.

6. Metacoxal sulcus arcuate and divergent from apical margin, ended medially in coxae or, if short, divergent from margin (Fig. 3A) (0); sulcus linear, complete or not, appressed to margin; if incomplete then not divergent from margin (Fig. 3B) (1).

7. Basal section of stria 1 present (0); absent (1).

8. Elytral setigerous lateral umbilicate puncture 2 in line with puncture 1 and 3(0); 2 distant from margin, separated from margin by a distinct convexity and mesad of 1 and 3 (1).

9. Elytral humeral tooth anterad and in line with interval 8, elytra across humeri broad and humeral angles sharp (0); tooth anterad interval 7, elytra with rounder and narrower humeral angles (1). Only the position of the tooth was scored. The general shape is not considered discrete.

10. Microsculpture on elytra reticulate and isodiametric (0); transversely elongate mesh (1).

11. Tarsal claws smooth (0); pectinate (Fig. 2A) (1).

12. Ventral setae of fifth tarsomere subequal in length (0); unequal in length, apical pair much longer (ca 2×) than subapical pair (1).

13. Pronotal basolateral region outside outer basal foveae convex (0); basolateral region flat and reflexed (1).

14. Pronotum front margin broad, front angles produced or not, separate from occiput (0); pronotum narrow, appressed to occiput, front angles not protruding (1).

15. Pronotal lateral bead narrow and of uniform width throughout, if narrowing

at all then narrowed just before hind angles (0); bead narrower in apical third, then broadened near middle and again narrowed near base, basal taper starts well before hind angles (1).

16. Pronotal disc microsculpture obsolete (0); transverse and faint, surface shiny (1); transverse and well developed, microlines clearly visible and surface slightly duller (2); reticulate and isodiametric mesh regular or somewhat irregular, surface dull (3) [nonadditive].

17. Microlines in and near basal fovea of pronotum obsolete (0); transverse and faint, surface shiny (1); transverse and well developed, microlines clearly visible and slightly duller (2); reticulate and isodiametric or somewhat irregular, surface dull (3) [nonadditive].

18. Transverse sulci on sterna V–VI complete across sternum (0); laterally present and medially absent (1); completely absent (2). This character was considered additive to set adjacency of states. State 1, interrupted medially, is equally similar to completely absent and entire.

19. Median lobe basal bulb unmodified, small and smoothly rounded (0); basal bulb enlarged and laterally sulcate (1).

20. Endophallus folding pattern and/or spine fields not visible in cleared lobe (0); endophallus folding and pattern and/or spine fields visible as darker regions in lobe (1). Only in a few specimens was the endophallus successfully everted. However, it is presumed that development of larger spines, lobes and scales, that can be seen through the median lobe, is a character that may group taxa. It is likely to be less informative than the multiple characters that potentially exist in the various structures of an everted endophallus, e.g., *A. basistriata* (Fig. 22E–I).

21. Blade of median lobe smooth ventrally (0); ventrally strigate (1).

22. Tip of median lobe tapered gradually to apex, not noticeably thin in lateral view (0); tip very thin in lateral view (1).

23. Apex of median lobe approximately symmetrically narrowed in dorsal view (0); apex distinctly asymmetrically produced to right (Fig. 22D) (1).

24. Blade of median lobe smoothly curved and uniformly tapered in lateral view, slightly curved in dorsal view (Fig. 21M–R) (0); blade uniformly thin from bend to tip in lateral view and straight and narrow in dorsal view (Fig. 23Q–R) (1).

25. Diverticulum of appended gland present (Fig. 20F) (0); diverticulum absent (Fig. 19B) (1).

26. Paired bursal glands absent (0); present (Fig. 5) (1).

27. Seminal canal straight and simple or few (<3) loose twists, duct relatively broad (Fig. 19E) (0); duct narrow with a few (4–5) tight twists along its length (Fig. 20A) (1); duct narrow with many tight twists along its length (Fig. 19D) (2). This character was set as additive to establish adjacency of similar states.

28. Receptaculum of spermatheca discrete from duct as an expanded, annulated in most species, reservoir (Fig. 19D) (0); receptaculum not distinct from duct (Fig. 20C) (1).

29. Spermatheca without basal bulb (0); base of spermathecal duct expanded as a bulb (Fig. 20B) (1).

30. Appended spermathecal gland spherical (0); elongate (1).

Results of Cladistic Analysis

Of the 100 search replications (mult*100), 40 found trees of length 88 steps. Of these 34 were unique arrangements. Swapping on these trees (max*) found

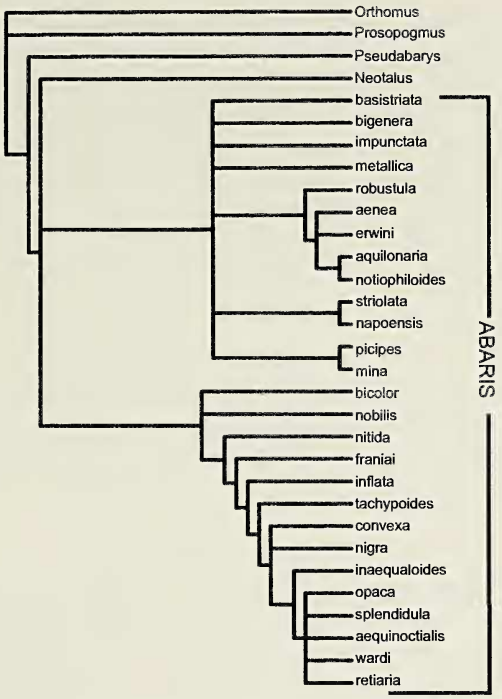

Fig. 30.—Consensus cladogram of the 36 MPTs of 88 steps.

two additional trees. A total of 36 most parsimonious cladograms was found (RI = 71, CI = 40, length 88 steps). These scores show that a reasonable level of grouping information is present and homoplasy is within the expected range (de Queiroz and Wimberger, 1993; Sanderson and Donoghue, 1989) for this matrix of taxa and characters.

The consensus cladogram (Fig. 30) is largely resolved, with monophyly for all clades named in the classification supported except the generic separation of *Neotalus* and *Abaris* and grouping of the members of the *A. picipes*-group.

In some resolutions *Neotalus* is placed as sister to *Abaridius*. This placement is not preferred as it is supported only by the lack of obvious structure of the endophallus of the median lobe and would require accepting the hypothesis that pectinate claws gained in the common ancestor of *Abaris* were lost in *Neotalus portai*. The endophallic structure is not known for most of the *Abaridius* species, absent in five species and is present in *A. nigra*. In other groups of Carabidae, and particularly in pterostichine clade taxa, the endophallus has been best used for differentiating between species and is assumed a less suitable system for generic distinction in abariform taxa.

A number of resolutions have the clade of *A. mina* + *A. picipes* placed as sister to the *A. striolata*-group. This placement is not preferred as the grouping is based only on the microsculpture of the head and requires parallel gains of a very similarly shaped and strigate median lobe in both *A. mina* + *A. picipes* and *A. basistriata*. Grouping *A. mina, A. picipes,* and *A. basistriata* minimizes homoplasy in the characteristic form of the median lobe. This preferred arrangement also minimizes the hypothesized number of origins of the long, narrow and tightly

twisted spermathecal canal. It does require a hypothesis that this peculiar form of spermatheca reversed to a simpler, straight form in *A. picipes*.

Little support exists for any particular arrangement of *Abaridius* species and thus relationships among them are largely unresolved in the consensus.

The selected cladogram (Fig. 31, 32) shows only clades supported by unambiguous character state changes. These groups are supported under both accelerated and delayed transformation optimizations. This arrangement is one of three that are consistent with my preferred placement of *Neotalus* and the clade of *A. mina* + *A. picipes*. These three differ only in the arrangement of the species within the *A. tachypoides*-group.

Interpretation of the Pattern

Based on the selected arrangement, it is possible to discuss the pattern in terms of evolutionary process. This involves extrapolation from the observed and summarized data to the likely conditions of the hypothetical ancestors and the character state transformation.

Character Evolution

Of the 30 characters included in the analysis based on my initial hypothesis of homology (Patterson, 1982; de Pinna, 1991), 12 are perfectly congruent (ci = 1.0) and can be considered to have passed the test of secondary homology (de Pinna, 1991) (Fig. 31, 32: characters 1, 2, 6, 8, 11, 12, 19, 21, 22, 25, 26, 30). Other characters show some homoplasy but still provide grouping information for some taxa as reversals or convergent origins of states, e.g., the loss of the basal section of stria 1 (Fig. 31: character 7) and the flat-reflexed baso-lateral margin of the pronotum (Fig. 31: character 13). States of only two characters (Fig. 31, 32: characters 14, 29) were shown to be entirely parallel occurrences of conditions not otherwise distinguishable.

The female reproductive tract has several interesting characters that define both generic and species level relationships. The paired dorsal glands of the bursa (Fig. 5) in species of the abariform genera are similar to those found in cicindelines (Deuve, 1993) and some platynines (Liebherr and Zimmerman, 1998), but are unique among all pterostichine taxa. The absence of the diverticulum is a return to the plesiomorphic condition for the pterostichines (Will, 2000), but is clearly a synapomorphic loss for *Neotalus* + *Abaris*. The form of the spermatheca is at once synapomorphic at some levels, e.g., for *A. aenea*-group + *A. picipes*-group clade, and convergent in pairs of different states. Pairing occurs in the *A. striolata*-group [state 0] and (*A. aenea*-group + *A. picipes*-group) [2, although reversed in some]; *A. mina* [0] and *A. picipes* [2]; *A. aquilonaria* [1] and *A. notiophiloides* [0]; and *A. splendidula* [1] and the terminal polytomy including *A. aequinoctialis* [0]. Since some of the species pairs are entirely sympatric, these strikingly different forms of the spermatheca may be indicative of differences in oviposition and/or mating behavior. The ovipositors, however, are almost identical in all species. Most of the variation in form of the bursa and spermatheca is found in species of *Abaris* s.str., e.g., *A. striolata*-group and *A. notiophiloides*. These taxa also have the greatest modifications of the male genitalia.

The male genitalia are quite simple in most species and with a trend toward a very simple, straight median lobe and unmodified endophallus in species of the subgenus *Abaridius*. Paralleling the modifications in the female reproductive tract,

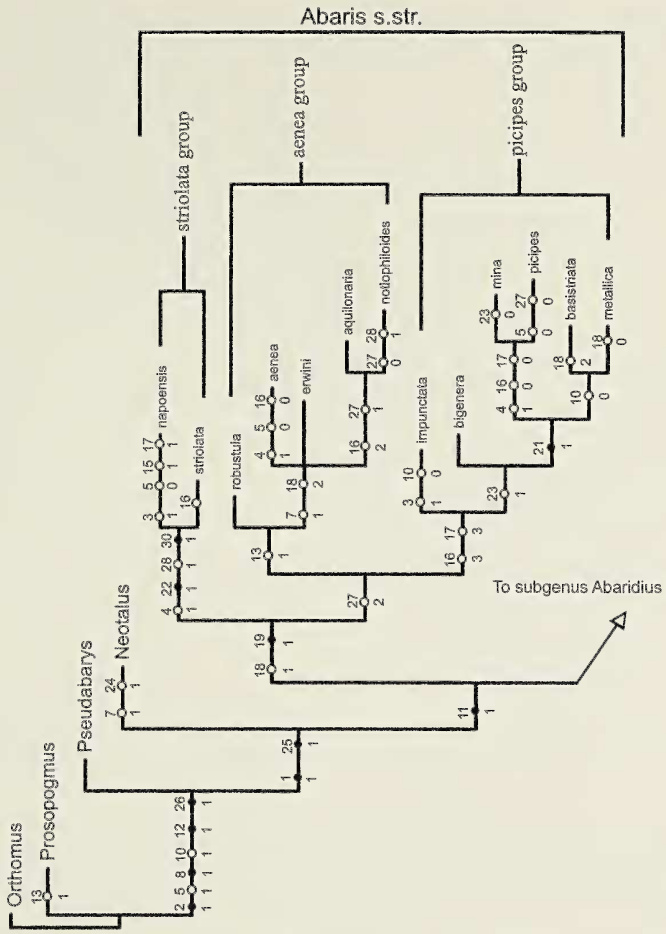

Fig. 31.—Portion of selected cladogram showing outgroup genera, *Neotalus* and *Abaris* (s.str.) species. Unambiguous character state changes are mapped on the cladogram, black discs—non homoplasious change, white—homoplasious change. Numbers above branches are character numbers, below are character state.

species of *Abaris* s.str. have smaller parameres, a relatively larger basal bulb of the median lobe, variously modified median lobe tip, and a spinose and lobed endophallus in some species.

Microsculpturing shows no clear transformation series and is highly homoplasious. From the cladogram one can only generalize that transverse (either faint, obvious or irregular) is in most clades plesiomorphic, and all the other states are frequently derived from it.

Biogeographical Overview

Plant and animal distributions in tropical America have been the data source for many studies on ecological and historical biogeography (see Whitmore and Prance, 1987). Carabid beetles are well represented in these studies (Shpeley and Ball, 1993; Noonan, 1985 and included references). The distribution of *Abaris*

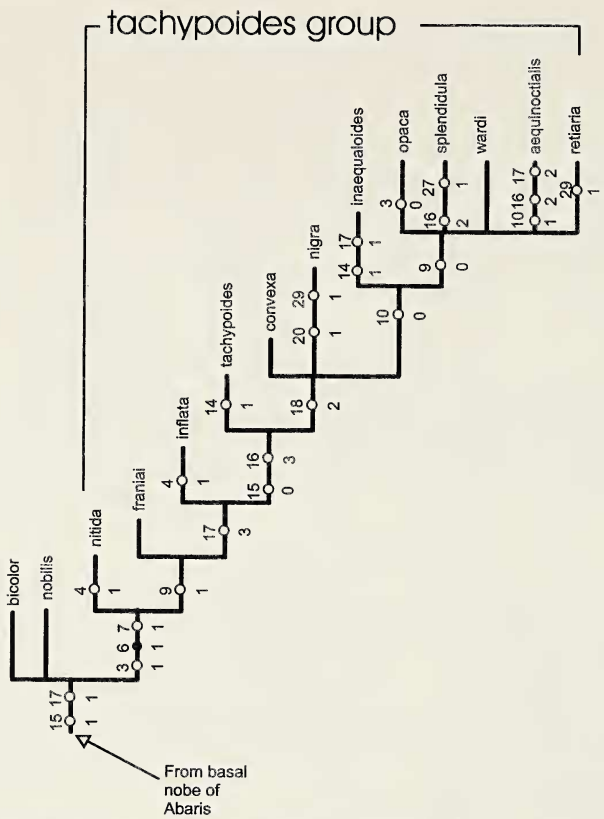

Fig. 32.—Portion of selected cladogram showing *Abaris* (*Abaridius*) species. Unambiguous character state changes are mapped on the cladogram, black discs—non homoplasious change, white—homoplasious change. Numbers above branches are character numbers, below are character state.

species includes the entire breadth of the New World tropics and so investigation of their pattern of distribution adds to our general understanding of the biogeography of animals in the New World.

Areas of Endemism

The "zoogeographic zones" presented by Shpeley and Ball (1993) for species of *Coptodera* Dejean, 1825 (Fig. 33, Table 1) are used in the biogeographic analysis and discussion of the distribution of *Neotalus* and *Abaris* below. The areas identified for *Coptodera* species, in general, correspond to the distribution of *Abaris* species and contain more or less identifying sets of taxa. Therefore it is reasonable to use these areas for cladistic biogeographic analysis from which descriptive patterns can be discussed.

In addition to the similar ranges, both *Abaris* and *Coptodera* have species that are found at fruit falls in tropical forest, many individuals are more or less metallic, and many have large eyes and pectinate claws. These similarities suggest an overlap in behavior or life histories. *Coptodera* species, however, are clearly associated with tree trunks, limbs and logs (Shpeley and Ball, 1993); whereas *Abaris* species are only known as ground dwellers. Adults of both genera pre-

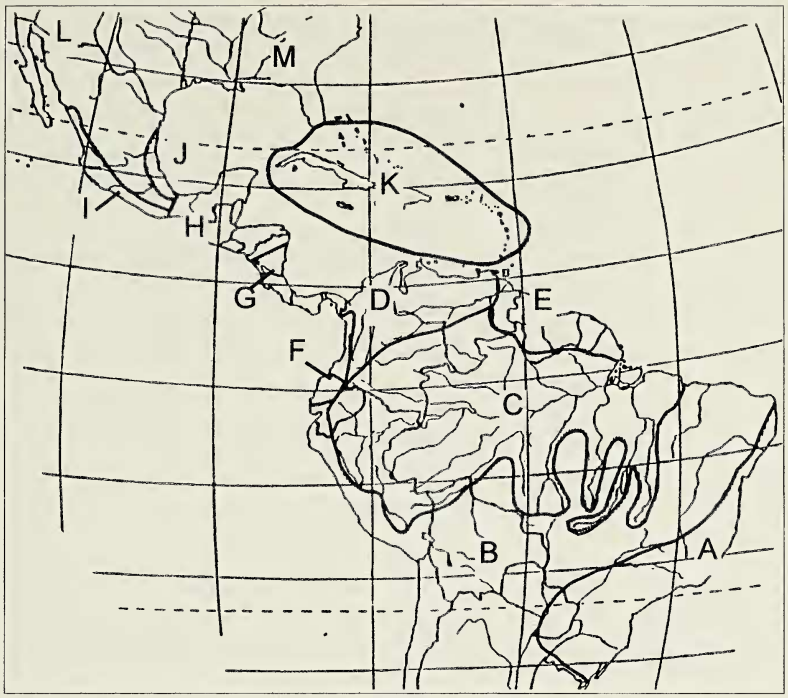

Fig. 33.—Zoogeographic zones in southern North America, the West Indies, Central and South America for *Abaris* and *Coptodera* species. From Shpeley and Ball (1993). See text for explanation of zones.

sumably fly; however, the more arboreal habits and the relatively more numerous records of flight for *Coptodera* species suggest its members fly more frequently.

Descriptive Aspects of Distributions

Refer to distribution maps of species for the following discussion (Fig. 10–17) and to table 1 and figure 33 for zones. Because of the paucity of material and limited number of collecting sites, the analysis of the biogeographical patterns for species of *Neotalus* and *Abaris* must assume the material in hand represents the ranges of species, and therefore the areas assigned to them in the analysis. Several species that have been sampled more adequately have large ranges, and in many cases are sympatric with one or more other species. The collection of more material, especially from the vast and under-collected areas in Brazil, may corroborate or call for revision of hypotheses presented here.

Most *Abaris* species (13 spp.) live entirely or in part in tropical lowland forests corresponding to zone C or the drier forests south of the Amazon Basin, zone B (11 spp.). Only four species, all members of the *A. picipes*-group, have ranges that extend southward beyond the tropics. *Abaris splendidula* is the only species that ranges north of the tropics. The range of *N. portai* also extends south of the tropics.

Members of the *A. aenea*-group and *A. picipes*-group show a marked divergence in habitat breadth. The *A. aenea*-group species are relatively stenotopic and found in moist tropical lowland forest from Bolivia to southern Mexico at ele-

Table 1.—*Zoogeographic zones from Shpeley and Ball (1993) used as areas for biogeographical analysis for* Abaris *and* Coptodera *species.*

Zone	Area
A	Southern Atlantic South America. Atlantic forest
B	cis-Andean South America south of Amazon Basin from eastern slope of Andes west of zone A
C	Amazon Basin
D	cis-Andean South America north of the Amazon Basin and west of zone E
E	cis-Andean South America north of the Amazon Basin including northern Brazil and the Guianas
F	Chocó refugium in trans-Andean Colombia and Ecuador
G	Lower Central America north to southern Nicaragua
H	Nuclear Central America from Nicaragua to the Isthmus of Tehuantepec in southern Mexico
I	Mexico north of the Isthmus of Tehuantepec, Pacific versant
J	Mexico north of the Isthmus of Tehuantepec, Gulf versant
K	West Indies
L	Southwest United States and northern Mexico
M	Eastern United States

vations of 100–970 m, with most specimens collected from between 200–400 m. In contrast, members of the *A. picipes*-group are centered in drier forests south of the Amazon Basin (zone B), are generally more widespread, and apparently eurytopic. The widespread *A. picipes*-group species have been collected at elevations of 100–1680 m (or as high as 3600 m, see discussion under *A. basistriata* above). In the *A. aenea*-group, *A. aenea* ranges into lower Central America and *A. aquilonaria* is found through nuclear Central America and into southern Mexico at elevations of 200–970 m. Similarly *A. bigenera* and *A.* (*Abaridius*) *aequinoctialis* are found through nuclear Central America and into southern Mexico. The former, like other *A. picipes*-group species, has been collected at a variety of elevations (200–1680 m) and in several habitat types. Conversely the latter, like the *A. aenea*-group species, has been found only at elevations less than 850 m. Most *Abaridius* species are known from zones B and C; only *A. aequinoctialis* and *A. splendidula* occur outside of South America. *Abaris splendidula* lives in drier and cooler habitats and, like the species of the *A. picipes*-group, can be found across a wide range of elevations (0–1100 m).

Biogeographic Analysis

Biogeography is a synthetic field that draws a constellation of data from other disciplines such as systematics, geology and ecology. Historical biogeography (Rosen, 1978:160) specifically attempts to reconstruct the origin of taxa and biotas based on the pattern of relationships found through the systematic study of taxa and the resulting implied genealogy. If each terminal taxon lived exclusively in one area then, the area relationships and historical pattern could be read by replacement of the taxa with their areas on the cladogram. However, distributional patterns are complicated by widespread taxa and redundant areas, i.e., sympatric species distributions (Page, 1990; Nelson, 1984).

Several methods have been proposed to reduce complex taxon-area cladograms to a fundamental area cladogram (Nelson and Platnick, 1981) in which areas occur only once. Component analyses include various conversion rules that make assumptions regarding missing areas, widespread taxa and redundant distributions

(Page, 1990). The methods include Assumption 0 (= Brooks parsimony analysis (BPA), Wiley, 1987); Assumptions 1, 2 (Nelson and Platnick, 1981), and three-area statements (TAS) (Nelson, 1991).

Assumption 0 (BPA) has been criticized as restrictive in its treatment of widespread taxa (Page,1990:124). Assumptions 1–2 are increasingly more realistic but because of memory handling limitations of the only available computer program, Component 1.5 (Page, 1989), the large number of hypotheses that can result from complex data under these assumptions makes analyses under these assumptions impossible to complete. TAS and three-taxon analysis (3TA) methods and implications have come under extensive criticism (Farris and Kluge, 1998).

An alternative parsimony criterion to the component based analyses is reconciled tree analysis or tree mapping (Page, 1990, 1994; Nelson and Platnick, 1981) (referred by some authors as a component analysis, e.g., Morrone and Carpenter, 1994:101). Although no criteria have been presented that allow for determining a single best method for biogeographical analysis (Morrone and Carpenter, 1994: 111), reconciled tree analysis as implemented in Component 2.0 is interpretable and practical means for analyzing biogeographical data and is used herein.

Reconciled tree analysis finds the best fitting pattern(s) of area relationships for the observed taxon-area cladogram by inserting terms (leaves or components (Page, 1993)) into a user-tree until the observed pattern is reconciled with the presumed area relationships. Three measures of fit for the reconciled tree that have been proposed are (Page, 1994), 1. duplications, 2. leaves added, and 3. number of losses.

"Real" duplication events manifest as redundant nodes (Page, 1994:65) and are explained as primitive sympatry or secondary dispersal events subsequently followed by vicariance (Liebherr and Zimmerman, 1998:157). Minimizing duplications results in a set of trees that generally includes trees produced by minimizing "leaves added", and so is equal to or larger than that set. The number of leaves added is often reported as items of error (IOE), to measure fit between two trees (Nelson and Platnick, 1981). IOE is readily calculated by doubling the number of leaves added to the observed tree. The measure is easily derived but biological interpretation of this measure is unclear (Page, 1994).

In regard to the reconciled tree, losses are supposed ancestral species that did not disperse into an area or became extinct before a vicariance event resulted in two areas. Thus, absence of potential descendant taxa is accounted for by a single event in the ancestor rather than an event for each leaf and component. This is most clearly thought of in a strictly cospeciational situation when a parasite is lost from a host through extinction. Counting leaves or using IOE may overestimate the number of such events (Page, 1988) by preferring the addition of leaves to reduce duplications. When a heuristic search is conducted for best fitting user-trees for a set of areas where dispersal is deemed likely, minimization of duplications and leaves is appropriate. Such is the case in the Hawaiian Islands (Liebherr and Zimmerman, 1998). In such a system, no preference for ancient versus recent extinction events is defensible.

Focusing on duplications and leaves can increase the number of losses. In a hypothetical example shown in figure 34, the single duplication of the user-tree in 34B requires 3 losses and 10 IOE (5 leaves added) to account for the observed occurrence of area II and its sister-area relationship with area III. Conversely figure 34A has the same number of leaves added (5 leaves = 10 IOE) as 34B, but the paraphyletic relationship of II+III requires one less loss than in 34B. In

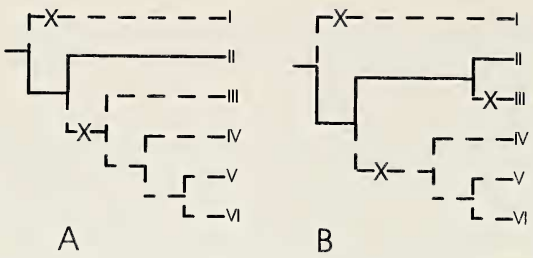

Fig. 34.—Hypothetical components from two reconciled trees for areas I–VI. Both represent a single duplication of the respective user-tree requiring 5 added leaves (dashed lines). Area II represents the occurrence of the area in the observed tree. Losses are mark with an "X." A. 2 losses. B. 3 losses.

the user-tree 34A, only 2 events (primitive losses or failure of the ancestor to disperse) are required.

In a system where vicariance and not dispersal is held to be the primary type of event, minimizing losses is a more reasonable parsimony criterion. By this method, more tree duplications are acceptable if they result in fewer losses (extinction events) during the history of diversification. This is reasonable for the large continental areas occupied by *Abaris* and *Coptodera* species. Using this criterion does not preclude dispersal as an explanation for parts of the resulting pattern that include duplications. However, these may be best explained as primitive sympatry and subsequent vicariance.

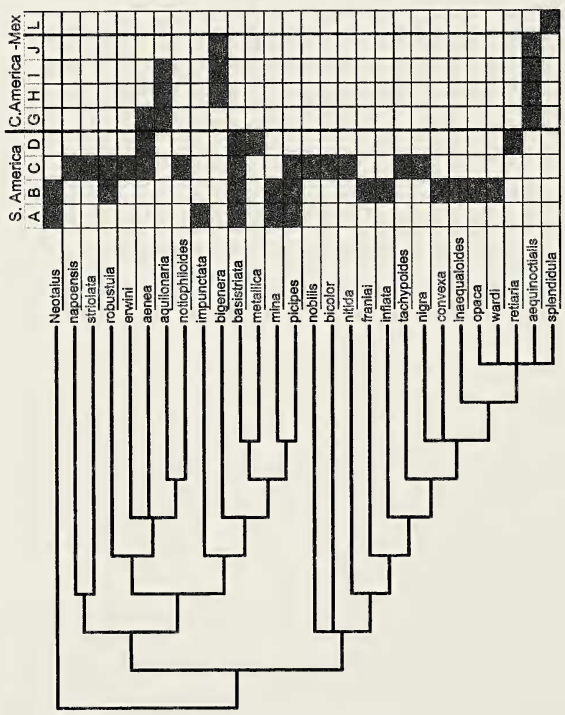

Fig. 35.—Taxon-area cladogram for *Neotalus* and *Abaris* species. See text and figure 33 for explanation of zones.

By looking at the areas relative to their relationships on the preferred cladogram (taxon-area cladogram Fig. 35), it is likely that the present distribution is the result of 4–5 separate dispersal/speciation events into or in Central America. Three pieces of evidence suggest that these dispersals are relatively recent, probably occurring no earlier than the early Pliocene when the Central American land bridge was formed (Stehli and Webb, 1985): 1. few *Abaris* species are present in Central America; 2. no species are found in the West Indies; and 3. all are apparently fully winged. This contrasts with other groups whose ancestors are presumed to have undergone earlier emigration from South America. These groups have greater numbers of Central American and Mexican species (e.g., *Coptodera* (Shpeley and Ball, 1993), *Pseudabarys* (Will, unpubl.)); species in the West Indies (e.g., *Coptodera*, *Dyschromus* (Erwin, 1979)); and/or species with brachypterous flight wings in some Central American species (e.g., *Dyschromus, Pseudabarys*).

When no preferred geological hypothesis is available, a heuristic search for a best fitting set of area relationships, a fundamental area cladogram, can be conducted using Component 2.0 (Page, 1993, 1994). Options used in heuristic search and reconciled tree analyses of *Coptodera* and *Neotalus* + *Abaris* included the following: 1. absence was treated as missing data, 2. widespread associates were mapped, 3. branch swapping used was nearest-neighbor interchange, 4. optimality criterion used was minimize losses.

Since the preferred cladogram contains unresolved nodes, Component necessarily resolves them arbitrarily before running the analysis. Allowing these arbitrarily resolved cladograms could permit the use of resolutions that are suboptimal in length. Therefore, a fully resolved cladogram (Fig. 36A) was constructed that was of length 88 steps and contained nearest geographic neighbors. The phylogenetic hypothesis for *Coptodera* also contained unresolved nodes (Shpeley and Ball, 1993, their figure 36). These polytomies were resolved following the species pairs found in the cladistic analysis of Liebherr (presented in appendix B of Shpeley and Ball, 1993; their figure 41A–B). Taxa and area cladograms were submitted to Component and a heuristic search conducted as described above. For the *Neotalus* + *Abaris* species, 196 rearrangements produced 14 area cladograms that equally minimized losses (47 losses, 24 duplications, 164 leaves added), and for *Coptodera* species, 66 rearrangements produced 3 area cladograms that equally minimized losses (99 losses, 36 duplications, 380 leaves added) (Fig. 37A–C). The two sets of area relationships were compared by using Component's quartet dissimilarity measure. Two of the 14 *Neotalus* + *Abaris* species cladograms were found to be more similar to the three *Coptodera* species cladograms than the others (Fig. 37B–C). These two cladograms were used to develop the general historical relationships of the areas and the hypotheses for the process leading to the current distribution of *Abaris*. The strict consensus was also found for each set of data (Fig. 36D, 37D).

Based on the consensus cladograms for the areas, *Neotalus* + *Abaris* diversified in South America first with vicariance of the Atlantic forest (zone A), followed by isolation of the Amazon Basin (zone C), and finally separation of the *cis*-Andean region (zone B). The latter may have remained in contact with zone D by way of habitats along the lower-mid elevation corridor west of the Amazon Basin. This hypothesized corridor would have species distributions like those seen today from Bolivia, Peru, Ecuador, and Colombia, e.g., *A. erwini* and *A. aenea* (Fig. 11, 14). Plausibly, the common ancestor of *Neotalus* + *Abaris* originated in southern South America and species were restricted there until the Pliocene. This

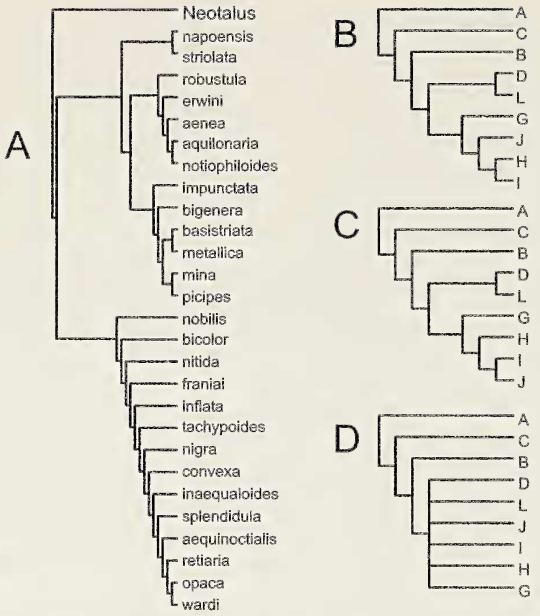

Fig. 36.—Cladograms for *Neotalus* + *Abaris* species and resulting relationships from biogeographical analyses. A. Fully resolved cladogram submitted to Component. B, C. Two of the 14 resulting fundamental area cladograms that were most compatible with the fundamental area cladogram derived from the Coptodera analysis. D. Consensus of the 14 fundamental area cladograms.

pattern and timing is similar to the hypothesis presented for ground beetles of the subgenus *Anisotarsus* Chaudoir, 1837 (*Notiobia* Perty, 1830) by Noonan (1981). However, *Abaris* would probably have been found in the subtropical and tropical habitats, as it is today, and not in the warm temperate habitats favorable to *Anisotarsus*.

The consensus cladogram (Fig. 36D) is not resolved for any of the Central American zones. This is a result of having only a few, primarily widespread species in these areas. If the two cladograms that are maximally similar to the results based on *Coptodera* are considered (Fig. 36B–C), the Central American and southern Mexican zones have separated sequentially from south to north. Unlike the results from the analysis of the *Coptodera* data, zones D, northern *cis*-Andean and zone L, northern Mexico + southwestern United States, are shown to have separated from the Central American zones. This suggest additional taxa may remain to be sampled in Central America that would provide evidence for area relationships similar to those resulting from the analysis of *Coptodera* species data.

By comparison, the pattern resulting from analysis of the *Coptodera* species shows a general pattern involving an early divergence of the northern and southern regions and then parallel differentiation proceeding within both sets of areas (Fig. 37A–D). Again, this is consistent with a group reaching proto-Middle America and North America earlier and more frequently than observed for *Abaris*. Such an early divergence (late Cretaceous or early tertiary) and frequent dispersals (10 events south to north) was proposed for *Coptodera* species by Shpeley and Ball (1993:162, 167).

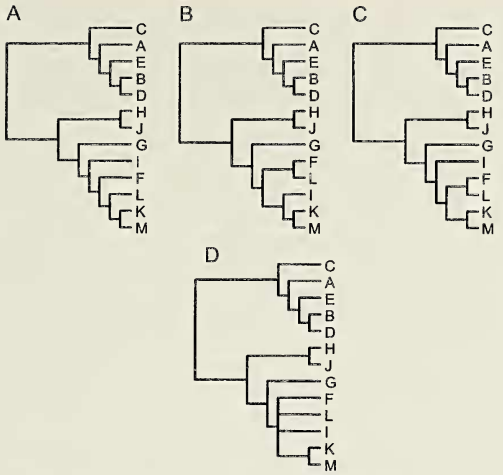

Fig. 37.—Resulting cladograms from the biogeographical analysis of *Coptodera* species. A, B, C. Three possible area relationships produced. D. Consensus cladogram of the three cladograms above.

It is surprising, given the apparent dispersal abilities of *Abaris* species (full flight wings and broad distributions of some species) that none have been found west of the Andes in the Chocó region (zone F) or on any island in the Carribean (zone K). Other carabid groups found in tropical lowland habitats, such as platynines, have established and diversified on all the Antilles (Liebherr, 1997). *Platynus* Bonelli, 1810 is species rich in the islands, *Glyptolenus* Bates, 1878 somewhat less diverse (Liebherr, 1997) and *Abaris* and *Pseudabarys* are completely absent, even from the island of Trinidad. Since *Abaris* is apparently no less vagile than these platynine taxa (some abariform taxa have been collected at lights and are known to fly). The difference may be related to biotic factors (likely for the islands of the West Indies) or inadequate collecting (probable for western South America).

Relative to apparently older elements (e.g., *Dyschromus*), the hypothesis that *Abaris* species simply did not reach northern South America until relatively recently may be sufficient explanation for their absence from the West Indies.

CONCLUSIONS

The monophyletic *Neotalus* + *Abaris* is revised. After necessary nomenclatural changes and the description of 17 newly recognized species (nearly tripling the species number of *Abaris*), the species of *Neotalus* and *Abaris* are now available to students of carabids and tropical biology. It is hoped that the ability to identify species will lead to more extensive study of their habits and perhaps studies that lead to a functional explanation for structures such as the paired bursal glands and pectinate claws.

The remaining abariform genus *Pseudabarys* stands, like *Abaris* stood, with few named species and many recognizable unnamed forms. Once these species are treated to the level of *Abaris*, a broader synthesis will be possible and hopefully another level of understanding reached in Neotropical pterostichine ground beetles.

ACKNOWLEDGMENTS

This project, which was part of my dissertation project at Cornell University, could not have been accomplished without the assistance of many people whose contributions, small or large, have been graciously accepted. For continuous support I thank Jim Liebherr and my other excellent and supportive committee members Quentin Wheeler and Melissa Luckow. I thank David Maddison, University of Arizona for support during preparation of the manuscript for publication. Numerous collection managers and carabidologists as listed in the materials section provided me with specimens and assistance along the way. Three individuals deserve special thanks. George Ball (UASM) made the monograph of *Abaris* possible by taking type specimens on loan from MHNP, providing copious notes regarding the specimens and reviewing the manuscript with great care. Bob Davidson (CMNH) was always a source of knowledge, specimens, solid review of my manuscript and not the least an excellent host. Yves Bousquet (CNCI) kindly provided valuable information on carabids in general and was particularly generous in allowing me to see data in his unpublished manuscripts and notes. He also provided a sound review of the manuscript. My successful fieldwork in Ecuador could not have been so, except for the assistance provided by Giovanni Onore (QCAZ), a man of great heart and benefactor of entomologists from throughout the world. It was Giovanni who wisely assigned Italo Tapia to assist me during my stay in Ecuador. Italo's impressive fortitude, sharp wit and willingness greatly enhanced my time in the field. At Cornell, Bryan Danforth and Tom Eisner both substantially assisted me with time and materials. An earlier version of the manuscript received an exceptionally thorough review by John Rawlins (CMNH). His efforts greatly improved this paper and his sage advice benefitted me personally. The project received generous financial support from National Science Foundation Doctoral Dissertation Improvement grant (DEB-9700764); A.C. Rawlins Endowment, Cornell University; Ernst Mayr research grant, Harvard University; G. Griswold Fund, Cornell University; and Palmer Assistantship, Cornell University.

LITERATURE CITED

AGASSIZ, J. L. R. 1846. Nomenclatoris Zoologici. Index Universalis, continens nomia systematica classium, ordinum, familiarum et generum animalium omnium, tam viventium quam fossilium, secumdum ordinem alphabeticum unicum disposita, adjectis homonymiis plantarum, nec non variis adnotationibus et emandationibus. Jent et Grassmann, Soloduri.

ALLEN, R. T. 1972. A revision of the genus *Loxandrus* LeConte (Coleoptera: Carabidae) in North America. Entomologica Americana, 46:1–184.

BALL G. E., AND Y. BOUSQUET. E. 2000. Carabidae Latrelle, 1810. Pp. 32–132, *in* American Beetles. Vol. 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia (R. H. Arnett, Jr., and M. C. Thomas, eds.). CRC Press, Boca Raton, Florida.

BATES, H. W. 1871. Notes on Carabidae, and descriptions of new species (no.1). Entomologist's Monthly Magazine, 7:218–224.

———. 1882. Insecta, Coleoptera, Carabidae, Vol 1, part 1. Pp. 40–152, plates iii–v, *in* Biologia Centrali-Americana (F. D. Godman and O. Salvin, eds.). Taylor and Francis, London.

BLACKWELDER, R. E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies and South America. Part I. Bulletin of the United States National Museum. No. 185.

BOUSQUET, Y. 1984. Redescription of *Abaris splendidula* (LeConte) new combination (Coleoptera: Carabidae: Pterostichini). The Coleopterists Bulletin, 38:384–389.

———. 1999. Supraspecific classification of the Nearctic Pterotichini (Coleoptera: Carabidae). Fabreries, supplement 9.

BOUSQUET, Y., AND A. LAROCHELLE. 1993. Catalogue of the geodephaga (Coleoptera: Trachypachidae, Rhysodidae, Carabidae including Cicindelini) of America north of Mexico. Memoirs of the Entomological Society of Canada, 167:1–397.

BOUSQUET, Y. AND J. K. LIEBHERR. 1994. Larval description of *Abaris bigenera* Bates, 1882, and notes on relationships of the genus *Abaris* Dejean, 1831 (Coleoptera: Carabidae: Pterostichini). Journal of the New York Entomological Society, 102:435–441.

CHENU, J. C. 1851. Encyclopédie d'histoire naturelle ou Traité complet de cette science d'après les travaux des naturalistes les plus eminents de tous les pays et de toutes les époques. Coléoptères, avec la collaboration de M. E. Demarest. Tome I. Marescq and Harvard Press.

CHAUDOIR, M. DE. 1852. Mémoire sur la famille des carabiques. 3e partie. Bulletin de la Société Impériale des Naturalistes de Moscou, 25:3–104.

———. 1873. Matériaux pour servir à l'étude des Féroniens. Bulletin de la Société Impériale des Naturalistes de Moscou, 47(2):85–116.

CSIKI, E. 1930. Carabidae: Harpalinae IV (Pars 112). *In* Coleopterorum Catalogus (W. Junk and S. Schenkling, eds). Junk, Berlin.

DEJEAN, P. F. M. A. 1831. Species général des Coléoptères de la collection de M. le Comte Dejean. Tome cinquième. Mequignon-Marvis, Paris.

DEJEAN, P. F. M. A., AND J. B. A. BOISDUVAL. 1832. Iconographie et histoire naturalle de Coléoptères d'Europe. Tome troisième. Mequignon-Marvis, Paris.

DE PINNA, M. C. C. 1991. Concepts and test of homology in the cladistic paradigm. Cladistics, 7: 367–394.

DE QUEIROZ, A., AND P. H. WIMBERGER. 1993. The usefulness of behavior for phylogeny estimation: Levels of homoplasy in behavioral and morphological characters. Evolution, 47:46–60.

DEUVE, T. 1993. L'abdomen et les genitalia des femelles de Coléoptrès Adephaga. Mémoires du Muséum National d'Histoire Naturelle, 155:1–184.

ERWIN, T. L. 1979. The American connection, past and present, as a model blending dispersal and vicariance in the study of biogeography. Pp. 355–367, *in* Carabid Beetles: Their Evolution, Natural History, and Classification. Proceedings of the First International Symposium of Carabidology (T. L. Erwin, G. E. Ball, D. R. Whitehead, A. L. Halpern, eds.). Junk, The Hague.

ERWIN, T. L. 1991. Natural history of the carabid beetles at the BIOLAT Biological Station, Rio Manu, Pakitza, Peru. Revista Peruana De Entomologia, 33:1–85

FARRIS, J. S., AND A. G. KLUGE. 1998. AThe brief history of three-taxon analysis. Cladistics, 14:349–362.

GEMMINGER, M., AND E. VON HAROLD. 1868. Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus. Tom. I Cicindelidae-Carabidae. Gummi, Monachii.

GOLOBOFF, P. 1994. Nona: a tree searching program. Program and documentation, distributed by James M. Carpenter, New York.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (ICZN). 1999. International code of Zoological Nomenclature. Fourth Edition. The Natural History Museum, London.

LACORDAIRE, J. T. 1854. Histoire naturelle des insectes. Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome premier contenant les familles des cicindélètes, carabiques, dytiscides, gyrinides, et palpicornes. Roret, Paris.

LAPORTE DE CASTELNAU, F. L. 1840. Histoire naturelle des insectes Coléoptères: avec une introduction renfermant l'anatomie et la physiologie des animaux articulés, par M. Brullé. Tome premier. Duméril, Paris.

LAWRENCE, J. F., AND E. B. BRITTON. 1994. Australian Beetles. Melbourne University Press, Melbourne, Australia.

LECONTE, J. L. 1863. New species of North American coleoptera. Prepared for the Smithsonian Institution. Part I. Smithsonian Miscellaneous Collection, 167:1–86.

LIEBHERR, J. K. 1986. *Barylaus*, new genus (Coleoptera: Carabidae) endemic to the West-Indies with Old-World affinities. Journal of the New York Entomological Society, 94(1):83–97.

———. 1997. Review of Antillean *Glyptolenus* Bates (Coleoptera: Carabidae), with description of a new species precinctive to St. Vincent. Studies in Neotropical Fauna and Environment, 32:89–99.

LIEBHERR, J. K., AND K. W. WILL. 1998. Inferring phylogenetic relationships within Carabidae (Insecta, Coleoptera) from characters of the female reproductive tract. Pp. 107–170, *in* Phylogeny and Classification of Caraboidea (Coleoptera: Adephaga). Atti del Museo Regionale di Scienze Naturali (G. E. Ball, A. Casale and A. Vigna Taglianti, eds.). Torino.

LIEBHERR, J. K., AND E. C. ZIMMERMAN. 1998. Cladistic analysis, phylogeny and biogeography of the Hawaiian Platynini (Coleoptera: Carabidae). Systematic Entomology, 23:137–172.

LORENZ, W. 1998. Systematic list of extant ground beetles of the world. (Insecta Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae). First edition. Published by the author, Tutzing, Germany.

MATTHEWS, M. 1998. The CSIRO vesica everter: A new apparatus to inflate and harden eversible and other weakly sclerotised structures in insect genitalia. Journal of Natural History, 32:317–327.

MOORE, B. P. 1965. Studies on Australian Carabidae (Coleoptera) 4.—The Pterostichinae. Transactions of the Royal Entomological Society of London, 117(1):1–32.

MORRONE, J. J., AND J. M. CARPENTER. 1994. In search of a method for cladistic biogeography: an empirical comparison of component analysis, Brooks parsimony analysis, and three-area statements. Cladistics, 10:99–153.

NELSON, G. 1984. Cladistics and biogeography. Pp. 273–293, *in* Cladistics: perspectives on the reconstruction of evolutionary history (T. Duncan and T. F. Stuessy, eds.). Columbia University Press, New York.

———. 1991. Three-area statements: standard assumptions for biogeographic analysis. Systematic Zoology, 40:470–485.

NELSON, G., AND N. PLATNICK. 1981. Systematics and biogeography: cladistics and vicariance. Columbia University Press, New York.

NIXON, K. C. 1999. Winclada, ver. 0.9.9 Published by the author, Ithaca, New York.

NIXON, K. C., AND Q. WHEELER. 1990. An amplification of the phylogenetic species concept. Cladistics, 6:211–223.

NOONAN, G. R. 1981. South American species of the subgenus *Anisotarsus* Chaudoir (Genus *Notiobia* Perty: Carabidae: Coleoptera). Part II: Evolution and biogeography. Contributions in Biology and Geology, Milwaukee Public Museum, 45:1–117.

———. 1985. Influences of dispersal, vicariance, and refugia on patterns of biogeographical distributions of the beetle family Carabidae. Pp. 322–349, *in* Taxonomy, Phylogeny and Zoogeography of Beetles and Ants (G. E. Ball, ed.). Junk, Dordrecht.

———. 1991. Classification, Cladistics, and Natural History of Native North American *Harpalus* Latreille (Insecta: Coleoptera: Carabidae: Harpalini), Excluding Subgenera *Glanodes* and *Pseudophonus*. The Thomas Say Foundation, Monograph 13.

PAGE, R. D. M. 1988. Quantitative cladistic biogeography: Constructing and comparing area cladograms. Systematic Zoology, 37:254–270.

———. 1989. COMPONENT version 1.5. Auckland, New Zealand.

———. 1990. Component analysis: A valiant failure? Cladistics, 6:119–136.

———. 1993. COMPONENT, version 2.0. Natural History Museum, London.

———. 1994. Maps between trees and cladistic analysis of historical associations among genes, organisms and areas. Systematic Biology, 43:58–77.

PATTERSON, C. 1982. Morphological characters and Homology. Pp. 21–74, *in* Problems of Phylogenetic Reconstruction, vol. 21 (K. A. Joysey and A. E. Friday, eds.). Academic Press, New York.

REICHARDT, H. 1977. A synopsis of the genera of Neotropical Carabidae (Insecta: Coleoptera). Quaestiones Entomologicae, 13:346–493.

ROSEN, D. E. 1978. Vicariance patterns and historical explanation in biogeography. Systematic Zoology, 27:159–188.

SANDERSON, M. J., AND M. J. DONOGHUE. 1989. Patterns of variation in levels of homoplasy. Evolution, 43:1781–1795.

SHPELEY, D., AND G. E. BALL. 1993. Classification, reconstructed phylogeny and geographical history of the New World species of *Coptodera* Dejean (Coleoptera: Carabidae). Proceedings of the Entomological Society of Ontario, 124:1–182.

SNODGRASS, R. E. 1935. Principles of insect morphology. McGraw-Hill, New York, New York.

STEHLI, F. G., AND S. D. WEBB. 1985. Chapter 1. A kaleidoscope of plates, faunal and floral dispersals, and sea level changes. Pp. 3–16, *in* The great American Biotic Interchange (F. G. Stehli and S D. Webb, eds.). Plenum Press, New York.

STORK, N. E. 1980. A scanning electron microscope study of tarsal adhesive setae in the Coleoptera. Zoological Journal of the Linnean Society, 68:173–306.

STRANEO, S. L. 1939. On the genus *Abaris* Dej. (Coleoptera: Carabidae). Psyche, 46:38–41.

———. 1941. Nuova specie del gen. *Bothynoproctus* Tschit. (Coleopt. Carab.) Bolletino della Societá Entomologica Italiana, 73:28–30.

———. 1977. Chiavi per la determinazione dei generi e sottogeneri dei Pterostichini dell'America del Sud (Coleoptera Carabidae). Bolletino della Societá Entomologica Italiana. Genova, 109:104–116.

———. 1979. Notes about classification of the South American Pterostichini with a key for determination of subtribes, genera and subgenera (Coleoptera: Carabidae). Quaestiones Entomologicae, 15:345–356.

TORRE-BUENO, J. R. DE LA. 1937. A Glossary of Entomology. Brooklyn Entomological Society, Brooklyn, New York.

TSCHITSCHÉRINE, T. 1898. Matériaux pour servir à l'étude des Féroniens. IV. Horae Societatis Entomologicae Rossicae, 32:1–224.

WHITMORE, T. C., AND G. T. PRANCE. 1987. Biogeography and Quaternary History in Tropical America, Clarendon Press, Oxford.

WILEY, E. O. 1979. An annotated Linneaen hierarchy, with comments on natural taxa and competing systems. Systematic Zoology, 28:308–337.

———. 1981. Phylogenetics. The Principles and Practice of Phylogenetic Systematics. John Wiley and Sons, New York, New York.

———. 1987. Methods in vicariance biogeography. Pp. 283–306, *in* Systematics and evolution: a

matter of diversity (P. Hovenkamp, E. Gittenberger, E. Hennipman, R. de Jong, M. C. Roos, R. Sluys and M. Zandee, eds.). Institute for Systematic Botany, Utrecht University.

WILL, K. W. 1999. Systematics and zoogeography of the genus *Lophoglossus* LeConte (Coleoptera Carabidae Pterostichini). Pp. 259–276, *in* Advances in Carabidology, Papers dedicated to the memory of Prof. Dr. Oleg L. Kryzhanovskij. Millenium Series. Entomology No. 1. (A. Zamotajlov and R. Sciaky, eds.). MUISO Publishers, Krasnodar.

———. 2000. Systematics and Zoogeography of Abaryform genera (Coleoptera: Carabidae: Pterostichini), and a phylogenetic hypothesis for pterostichine genera. Unpublished doctoral dissertation. Cornell University, Ithaca, New York.

WILL, K. W., A. ATTAGALLE, AND K. HERATH. 2000. New defensive chemical data for Ground Beetles (Coleoptera: Carabidae): interpretations in a phylogenetic framework. Biological Journal of the Linnean Society, 71:459–481.

———. 2001. Erratum, New defensive chemical data for Ground Beetles (Coleoptera: Carabidae): interpretations in a phylogenetic framework. Biological Journal of the Linnean Society, 73:167–168.

APPENDIX 1

Characters 1–30

	5	10	15		20	25	30
Orthomus	00010	00000	00000	030	00	00000	00000
Prosopogmus	00000	00000	00100	220	01	00000	00000
Pseudabarys	01001	00101	01000	120	01	00000	10000
Neotalus	11001	01101	01000	220	00	00011	10000
aenea	11010	01101	11100	022	11	00001	12000
aequinoctialis	11101	111*1	11000	222	00	00011	10100
aquilonaria	11001	01101	11100	222	11	00001	11000
basistriata	11001	00100	11000	332	11	10101	12000
bicolor	11001	00101	11001	110	??	?????	?????
bigenera	11001	00101	11000	331	11	00101	12000
convexa	11101	11111	11000	332	00	0000?	?????
erwini	11001	01101	11100	122	11	00001	12000
franiai	11101	11111	11001	110	??	?????	?????
impunctata	11101	00100	11000	331	11	0000?	?????
inaequaloides	11101	11110	11010	312	??	?????	?????
inflata	11111	11111	11001	130	??	?????	?????
metallica	11001	00100	11000	330	??	?????	?????
mina	11011	00101	11000	001	11	10001	12000
napoensis	11110	00101	11001	111	11	01001	10101
nigra	11101	11111	11000	332	01	00001	10010
nitida	11111	11101	11001	110	??	?????	?????
nobilis	11001	00101	11001	110	??	?????	?????
notiophiloides	11001	01101	11100	222	11	00001	10100
opaca	11001	11100	11000	332	??	?????	?????
picipes	11010	00101	11000	00(1,2)	11	10101	10000
retiaria	11101	11100	11000	332	00	00011	10?1?
robustula	1100*	00101	11100	121	11	00001	12000
splendidula	11101	11100	11000	232	00	00001	11000
striolata	11011	00101	11000	221	11	01001	10101
tachypoides	11101	11111	11010	330	00	0000?	?????

wardi	11101	11100	11000	332	00	00011	10100

State unknown = ?, Polymorphic = *.

APPENDIX 2

The Nexus File Submitted to Component 2.0 for Neotalus + Abaris

```
#NEXUS
BEGIN TAXA;
    DIMENSIONS NTAX=9;
    TAXLABELS
        A
        B
        C
        D
        G
        H
        I
        J
        L
    ;
ENDBLOCK;

BEGIN DISTRIBUTION;
    TITLE='BLOCK 1';
    NTAX=28;
    RANGE
        nap     : 3,
        str     : 3,
        rob     : 2 3,
        erw     : 3,
        aen     : 3 4 5,
        aqu     : 5 6 8,
        not     : 3,
        imp     : 1,
        big     : 6 7 8,
        bas     : 1 2 3 4,
        met     : 4,
        min     : 1 2,
        pic     : 1 2 3,
        nob     : 3,
        bic     : 3,
        nit     : 3,
        fra     : 2,
        inf     : 2,
        tac     : 3,
        nig     : 3,
        con     : 2,
        ine     : 2,
        spl     : 9,
        aeq     : 5 6 7 8,
```

```
            ret         : 4,
            opa         : 2,
            war         : 2,
            Neo         : 1 2
;
    TREE  T1=(28,(((1,2),((3,(4,(5,(6,7)))),(8,(9,((10,11),(12,13)))))),(14,(15,
                (16,(17,(18,(19,(20,(21,(22,(23,(24,(25,(26,27))))))))))))));
ENDBLOCK;
BEGIN TREES;

[!>Heuristic search settings:
> Trees fitted to block BLOCK 1
> Absence is treated as missing data
> Widespread associates mapped
> Nearest neigbor interchange (NNI) branch swapping performed
> Total number of rearrangments tried = 196
> Criterion minimised = number of losses
> Trees found = 14
> Minimal value = 45
]

    TRANSLATE
        1 A,
        2 B,
        3 C,
        4 D,
        5 G,
        6 H,
        7 I,
        8 J,
        9 L
    ;
    TREE  T1=(1,(3,(2,(4,(5,(9,(8,(6,7))))))));
    TREE  T2=(1,(3,(2,(4,(5,(9,(7,(6,8))))))));
    TREE  T3=(1,(3,(2,(4,(5,((6,8),(7,9)))))));
    TREE  T4=(1,(3,(2,(4,(5,(9,(6,(7,8))))))));
    TREE  T5=(1,(3,(2,(4,((5,9),(8,(6,7)))))));
    TREE  T6=(1,(3,(2,(4,(9,(5,(8,(6,7))))))));
    TREE  T7=(1,(3,(2,(4,((5,9),(7,(6,8)))))));
    TREE  T8=(1,(3,(2,(4,(9,(5,(7,(6,8))))))));
    TREE  T9=(1,(3,(2,(4,((5,(6,8)),(7,9))))));
    TREE  T10=(1,(3,(2,(4,((5,9),(6,(7,8)))))));
    TREE  T11=(1,(3,(2,(4,(9,(5,(6,(7,8))))))));
    TREE  T12=(1,(3,(2,((4,9),(5,(8,(6,7)))))));
    TREE  T13=(1,(3,(2,((4,9),(5,(7,(6,8)))))));
    TREE  T14=(1,(3,(2,((4,9),(5,(6,(7,8)))))));
ENDBLOCK;
```

The Nexus File Submitted to Component 2.0 for Coptodera

```
#NEXUS
BEGIN TAXA;
```

```
    DIMENSIONS NTAX=13;
    TAXLABELS
        A
        B
        C
        D
        E
        F
        G
        H
        I
        J
        K
        L
        M
    ;
ENDBLOCK;

BEGIN DISTRIBUTION;
    TITLE='BLOCK 1';
    NTAX=43;
    RANGE
        sal     : 8 10,
        ver     : 3,
        nisig   : 3,
        lin     : 7 8 9 10,
        sch     : 3 4 7 8,
        rel     : 3,
        elon    : 7 8 10,
        nvir    : 8 10,
        sah     : 1 2 3,
        meg     : 3,
        ruf     : 1 5,
        cham    : 6 7,
        chal    : 3,
        pic     : 1 2 3 4 5 7 8 10 11 13,
        fov     : 10,
        poe     : 7,
        aen     : 3 5,
        aer     : 13,
        vir     : 9,
        pak     : 3,
        way     : 3,
        acu     : 1 3 4 5 6 7 8 10,
        apic    : 6,
        sto     : 7,
        fest    : 3 7 8 9 10 11 13,
        drom    : 1 2 3 5,
        nit     : 1 2 3 5 6 7 8 9 10 12,
        brun    : 8 10 12,
```

```
            erw         : 3,
            ema         : 1 2 3 5,
            nig         : 3 5,
            teut        : 1,
            braz        : 1,
            aur         : 8 10,
            dep         : 1 2 4,
            cup         : 1 2 7 8 10,
            sig         : 1,
            squ         : 1,
            tran        : 1 2 3 4 7 8 9 10,
            ful         : 1,
            bif         : 1,
            xan         : 8 9,
            tri         : 1 3;
      TREE  T1=((1,((7,((5,10),(12,23))),(42,(19,34)))),((2,35),(((26,(3,(40,(31,(4,
                  24)))))),(39,(37,38))),((9,((16,(6,20)),(25,(15,(8,(11,32)))))),((17,
                  ((13,(22,30)),((33,36),(41,43)))),(14,((21,(18,29)),(27,28)))))));
ENDBLOCK;
BEGIN TREES;

[!>Heuristic search settings:
> Trees fitted to block BLOCK 1
> Absence is treated as missing data
> Widespread associates mapped
> Nearest neigbor interchange (NNI) branch swapping performed
> Total number of rearrangments tried = 66
> Criterion minimised = number of losses
> Trees found = 3
> Minimal value = 99
]

      TRANSLATE
            1 A,
            2 B,
            3 C,
            4 D,
            5 E,
            6 F,
            7 G,
            8 H,
            9 I,
           10 J,
           11 K,
           12 L,
           13 M
      ;
      TREE   T1=((3,(1,(5,(2,4)))),((7,(9,(6,(12,(11,13))))),(8,10)));
      TREE   T2=((3,(1,(5,(2,4)))),((7,((6,12),(9,(11,13)))),(8,10)));
      TREE   T3=((3,(1,(5,(2,4)))),((7,(9,((6,12),(11,13)))),(8,10)));
ENDBLOCK;
```